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Origin and phylogeny of the Cretaceous thoracican cirripede family Stramentidae

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A cladistic analysis of basal scalpellomorph cirripedes was undertaken in order to identify the phylogenetic position of the Stramentidae. This yielded a well-supported tree, in which the family is positioned crownwards of Archaeolepas, but basal to the families Scalpellidae and Zeugmatolepadidae. A new genus, Loriodepas, is described to accommodate some species previously referred to Archaeolepas. Basal scalpellomorphs display a remarkable change in shell mineralogy from calcium phosphate to calcium carbonate (Eolepas to Archaeolepas); the latter group is identified as a monophyletic clade, the Thoracicalcarea nov. A revised taxonomy of the predominantly Late Cretaceous cirripede family Stramentidae is presented. Stramentidae are subdivided into two subfamilies, Loriculinae subfam. nov., and Stramentinae, based on characters of tergum, carinolatus and peduncular plates. The former subfamily includes Loriculina Dames, 1885, Metaloriculina gen. nov. and, doubtfully, Blastolepas Drushchits & Zevina, 1969, and three new species are described, Loriculina ifrimae sp. nov., Metaloriculina stramentioides sp. nov and Metaloriculina norvicensis sp. nov. The Stramentinae include Leweslepas gen. nov., Stramentum Logan, 1897 and Parastramentum gen. nov. New species are Leweslepas hattinii sp. nov., L. hauschkei sp. nov., L. wrightorum sp. nov., Parastramentum albertaensis sp. nov., P. brydonei sp. nov., P. peakei sp. nov., Stramentum aleksievii sp. nov. and S. praecursor sp. nov. Cladistic analysis of the Stramentidae, based on 25 characters, supports the monophyly of the family, but relationships between subfamilies and genera are poorly resolved. However, in north-west Europe there is an evolutionary morphoclone, stratigraphically calibrated, from the early Cenomanian Leweslepas hauschkei gen. et sp. nov. through the middle Cenomanian Stramentum praecursor sp. nov. to the late Cenomanian–Turonian S. pulchellum. A split from this lineage is found in the Western Interior Basin of North America, and the early Turonian S. canadensis gave rise to the middle Turonian S. elegans, which lived epibenthically. Stramentum elegans gave rise to Parastramentum gen. nov.

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**Keywords**: cirripedes; Cretaceous; Stramentidae; phylogeny

Introduction

Stramentids, comprising the genera Stramentum Logan, 1897 and Loriodepas Dames, 1885, are a distinctive group of Cretaceous (predominantly Late Cretaceous) pedunculate cirripedes usually found attached to ammonite shells or, more rarely, to the benthic bivalve Inoceramus (Hattin & Hirt 1991). Their rarity, distinctive shape and pleasing appearance have led to a fairly extensive literature which describes numerous species. The overall outline of these cirripedes is oval, and they are laterally compressed and possess a peduncle covered by eight columns of large, alternating and imbricating plates. The low capitulum is made up of 12 plates, including a carina, a rostrum and paired scuta, terga, upper laterals and carinolaterals (Hattin 1977; Hattin & Hirt 1991). The genus Stramentum is widely distributed, having been recorded from the Cenomanian to Campanian at localities in Canada (Whiteaves 1889), the USA (Logan 1897; Withers 1945; Hattin 1977; Hattin & Hirt 1991), Mexico (Vega et al. 2007; Ifrim et al. 2011), Columbia (Royo y Gomez 1941; Villamil & Arango 1998), Japan (Nomura et al. 2006), Nigeria (Collins 1986), Algeria (Davadie & Emberger 1955), the Czech Republic (Kočová Veselská et al. 2013), Germany (Hauschke 1994; Hauschke et al. 2011; Jagt 2013), France (Breton & Boiné 1993), the United Kingdom (Withers 1935) and Lebanon (Dames 1885). In contrast, Loriodepas is very poorly known from two incomplete immature individuals, one from Lebanon (Dames 1878) and the other from Germany (von Zittel 1885), and a small number of isolated plates referred to the genus are recorded from England, Germany and France (Withers 1935).

The origin of the Stramentidae has been suggested to lie either in the Jurassic—Early Cretaceous genus Archaeolepas von Zittel, 1885, or in Zeugmatolepas Withers, 1913 (Withers 1935). Some species of Archaeolepas evidently possessed a peduncle similar to that of stramentids, with eight columns of imbricating, interdigitating plates, but...
the capitulum is made up of only six plates (carina and rostrum, plus paired scuta and terga). In *Zeugmatolespas*, there are very many small rows of lateral plates, and the capitulum includes at least 34 valves. Withers (1935) was impressed by the similarity between *Zeugmatolespas* and *Stramentum* in the high positions of the carinolatus and upper latus, and suggested this as a possible origin of *Stramentum*, by reduction of valve numbers.

Articulated stramentids are usually rare fossils, preserved by rapid burial in oxic benthic environments and by ammonites settling post mortem on anoxic sea floors (Hauschke et al. 2011; Ifrim et al. 2011), or more rarely by overgrowth by the ammonite host (Drushchits & Zevina 1969; Wittert 1996). However, in the Western Interior Basin of the USA, the Turonian species *S. elegans* Hattin, 1977 lived attached mostly to benthic bivalves (Inoceramidae), more rarely to empty ammonite shells (Hattin & Hirt 1991). Isolated plates have proved to be common in residues of Late Cretaceous sediments, and provide important information, not accessible in the articulated specimens which are usually crushed.

The present paper has two aims: (1) to clarify relationships amongst basal scalpellomorphs in order to establish the likely phylogenetic position of the Stramentidae; and (2) to describe the taxonomy and phylogeny of this family on the basis of extensive new material. The paper is one in a series redescribing Jurassic and Cretaceous thoracicans from the UK and elsewhere (Gale 2014a, b; Gale & Sørensen 2014, 2015). This revision was initially stimulated by the discovery of new articulated stramentids from the Cenomanian Lower Chalk of Lewes, Sussex, as well as by subsequent important finds in the Coniacian of Mexico (Ifrim et al. 2011) and the upper Campanian Chalk of Norfolk, UK.

**Institutional abbreviations**

BM: Booth Museum, Brighton, UK; CPC: Museo del Desierto, Saltillo, Coahuila, Mexico; KU: University of Kansas; MHNH: Muséum d’Histoire Naturelle du Havre, France; NHMUK: Natural History Museum, UK; OUM: Oxford University Museum, UK; PIMUZ: Paläontologisches Institut und Museum, Universität Zürich, Switzerland; SM: Sedgwick Museum, Cambridge, UK.

**Homology and terminology of scalpellomorph cirripede plates**

**Valve mineralogy**

Although it has been generally thought that scalpellomorph barnacles have always possessed a shell mineralogy of calcite (e.g. Newman et al. 1969), Höeg et al. (1999) argued that the Late Triassic—Early Cretaceous genus *Eolepas*, widely believed to be a basal scalpellomorph (Newman 1987; Buckeridge & Newman 2006), had a primary phosphatic composition and is preserved as the mineral francolite. This was challenged by Buckeridge & Newman (2006), who suggested that the material was possibly either a secondary replacement by calcium phosphate, or primary calcium hydroxyapatite, as reported from the primitive thoracican *Ibla* (Lowenstam et al. 1992; Lowenstam & Weiner 1992). However, Reid et al. (2012) used solid state nuclear magnetic resonance (SSNMR) to identify the composition of valves of *Ibla cumingi* Darwin, 1851 as a new, unique, poorly ordered hydrogen phosphate-like material.

Preliminary investigation of two well-preserved species of *Eolepas* (*E. rhaetica* Moore, 1861 and *E. bathonica* Withers, 1928) and the Late Carboniferous *Praelepas jaworskii* Chernyshev, 1930, using an ion probe, confirms the presence of abundant phosphorus in valve mineralogy (Koci et al. 2015; Gale & Schweigert in prep.). This has significance for the origin and basal evolution of scalpellomorphs, because *Eolepas* has been placed in the same family as *Archaeolepas*, the putative ancestor of the Stramentidae (Buckeridge 1983; Buckeridge & Newman 2006). The valves of *Archaeolepas*, stramentids, calanticids and scalpellids are all made of calcite, as are those of all extant balanomorphs and scalpellomorphs (Bourget 1987).

**Capitulum**

In the Ibliformes, only paired scuta and terga are present (Darwin 1851b; Buckeridge & Newman 2006; see Figs 1E, 2A), but the Late Carboniferous *Praelepas* (Figs 1A, B, 2B) also possessed a carina. The Triassic—Early Cretaceous *Eolepas* has been reconstructed with a rostrum (Withers 1928, fig. 64) and this image has been reused (Newman et al. 1969; Buckeridge 1983). Höeg et al. (1999) claimed that *Eolepas* lacked a rostrum, but without supporting evidence or illustration. In my view, supported by Buckeridge & Newman (2006) and Dr Günter Schweigert (pers. comm., July 2014), a rostrum is present, and this can be seen in an articulated individual of *E. aalenensis* (Richardson, 1908) from the Bajocian of Switzerland (Schweigert 2014; refigured here, Fig. 1C). This specimen, and another individual from the Bathonian of Normandy (Fig. 1D), are used to make a new reconstruction of *Eolepas* (Fig. 2C).

In the Ibliformes, the shape of the scuta and terga is triangular (Buckeridge & Newman 2006, fig. 2), the terga being tall and narrow in *Ibla* but relatively broad in *Neoibla*, *Idioibla*, *Chaetolepas* and *Chitinolepas*. The umbo is apical to subapical, and primordial valves on both the tergum and scutum have been described in *Idioibla pygmaea* (Broch 1922); such are visible on species of *Chaetolepas* and *Chitinolepas*. Terga in *Ibla* are tall, triangular and incurved towards the scutum (Fig. 1E), but in the other genera the nearly straight scutal/tergal boundary is
inclined ventrally, and a low, triangular tergum, with a convex occludent margin, sits like a cap above the scutum (e.g. *Idioibla*; Fig. 2A).

In *Praelepas*, the tergum is similar in shape and position to that of *Idioibla* (Fig. 1A, B) but the scutum is pentagonal with a subcentral umbo. The triangular, concavo-convex carina contacts the carinal margin of the scutum, and the base of the occludent margin of the tergum (Figs 1A, B, 2B). In *Eolepas*, the carina is similar to that in *Praelepas*, but the tergum is tall and rhombic, with a well-marked apicobasal ridge. The scuta of *Eolepas* are taller than broad and triangular, and the occludent margin is gently convex. The carina contacts only the tergum, along the long carinal margin, and a low, triangular rostrum is present (Fig. 1C).

The capitulum of calcitic scalpellomorphs always includes paired scuta and terga, a rostrum and a carina (Darwin 1851b; Newman et al. 1969; see Fig. 2D–F). The terga are typically rhombic, with an acute basal angle, and are very similar to those of *Eolepas*, but in *Stramentum* the tergum is triangular (Fig. 2E). In *Archaolepas*, *Loriolepas* gen. nov. and *Bosquetlepas* Gale in Gale & Sørensen, 2015, the terga have a short, straight basal margin. The scuta are typically triangular, taller than broad, with an apical umbo (Fig. 1D, E), but in *Stramentum* the scuta are trapezoidal with a subapical umbo (Fig. 2E; Hattin 1977).

The carina in *Archaeolepas*, *Loriolepas* gen. nov. and *Bosquetlepas* is triangular, taller than broad and variably concavo-convex. It is narrow, tall and flat in *Stramentum* (Hattin 1977). Scalpellid carinae are morphologically more complex, with differentiated parietes, intraparietes and a flat to convex tectum (Withers 1935). The carina contacts the tergum alone in *Archaeolepas* and *Loriolepas* gen. nov. (Figs 2, 3, 4), but in *Stramentum* it contacts only the carinolatus (Fig. 2E), and in scalpellids it contacts the carinolatus, the upper latus and the tergum (Fig. 1F).

*Archaeolepas* (Fig. 3), *Loriolepas* gen. nov. (Fig. 4) and *Bosquetlepas* completely lack lateral plates, but in *Stramentum* a triangular upper latus sits between the carina and tergum, and a carinolatus is present between the tergum and carina (Fig. 2E). The lower margins of these plates, with the exception of the tergum, contact peduncular plate columns (see below). In scalpellids, the pattern of lateral plates is highly distinctive and very consistent, including an upper latus, a carinolatus and a rostrolatus, which alternate with the capitular plates, and a lower inframedian latus, set beneath the upper latus and between the carinolatus and rostrolatus (Fig. 2F; Newman et al. 1969).

In pollicipedids, zeugmatolepadids and calanticids, lower whorls of lateral plates are also present, often including a subcarina, a subrostrum and other, unnamed plates. The ontogenetic sequence of introduction of the lateral plates was illustrated in *Pollicipes* by Broch (1922).

It has long been considered likely that the lateral plates of scalpellomorphs originated by upward transfer of peduncular plates from the top of respective columns (Darwin 1851b; Newman 1987), and this seems probable, even if it is virtually untestable. It can be argued that the upper latus was the first lateral plate to be acquired, as it is the only plate retained after secondary loss of the other laterals in forms such as *Neolepadidae* (e.g. Newman 1979); it is triangular, covers the junction between the scutum and tergum, and presumably affords valuable protection to this contact.
The terminology of the capitular valves of the Stramentidae was discussed and summarized by Hattin (1977, fig. 2), and his nomenclature is largely followed here (see Fig. 8). However, a few modifications are considered necessary; Hattin used the term ‘rostral slip’ for the depressed rostral surface of the scutum with which the inner lateral margin of the rostrum articulates in *Stramentum elegans*, in allusion to Darwin’s (1851a) use of ‘tergal slip’ for the reduced surface of the scutum in species of *Brachylepas* (Gale & Sørensen 2014). The term ‘rostral articulation surface’ is preferred here. The development of this surface varies from a poorly defined depressed area, to a discrete, sharply defined, slightly inset area in *Parastramentum* gen. nov.

**Peduncle**

Primitively, thoracicans lack peduncular plates, and these are absent in *Ibla*, *Praelepas* and *Eolepas* (see Fig. 2A–C; Withers 1928; Newman *et al.* 1969; Buckeridge & Newman 2006). The peduncle of extant scalpellomorph cirripedes is made up of columns of plates which form at the boundary between the peduncle and capitulum, usually after the full complement of capitular plates have been added (Newman & Ross 1998; Young 2001). This is true in all taxa studied, with the exception of the scalpellid *Scalpellopsis* (Young 2001) in which peduncular plates are added before the final laterals. Thus, the youngest plates are usually found at the contact with the capitulum. The
plates in scalpellids are added alternately in two series, scl-sr (scutal-lateral-subrostral) and rl-cl (rostrolateral carinolateral), which correspond with the eponymous capitular plates. Plesiomorphically, eight columns of plates are present (Newman & Ross 1998; Young 2001), but some scalpellids have reduced the number, and calanticids and pollicipedids have generated a very large number of small plate rows (Young 2001). The peduncle of the Late Mesozoic Stramentidae is covered by eight columns of large, robust plates, which are broader than tall, and the columns usually alternate and rarely abut, and thus conform with the presumed plesiomorphic condition.

In the type species of Archaeolepas, A. redtenbacheri (von Zittel, 1885), eight columns of peduncular plates have also been identified, and reconstructions of the genus have followed Withers’s original interpretation (1928, fig. 64; see also Newman et al. 1969; Buckeridge 1983). However, a re-examination of the original material of A. redtenbacheri has shown that 10 columns were present (Fig. 3), and in other species previously referred to Archaeolepas numerous columns are seen (Fig. 4). Therefore, it is necessary to discuss the homology of peduncular plate columns in basal scalpellomorph evolution, and the likely transitions to the condition in more derived scalpellids and calanticids.

In Archaeolepas redtenbacheri (Fig. 3) the peduncle is made up of 10 columns of alternating plates, which comprise two carinal columns (c1, c2), one which contacts the
base of the tergum (t), two columns which contact the basal margin of the scutum (s1, s2), and a rostral column (r). The plates of the s1, s2, t and c2 columns are crescentic with a flat to slightly concave basal margin and a rounded upper margin; they are two to three times broader than tall, and interdigitate internally and imbricate strongly (Fig. 3), such that only the upper portion is usually visible on the exterior. The general arrangement and shape of the plates is similar to that in stramentids, which, however, only ever have eight columns (Hattin 1977).

The evolution of lateral plates evidently necessitated significant changes in the position and relative size of the peduncular plate columns. The evolution of the upper latus as a cover over the scutal—tergal junction would only be effective if there was a sideways shift in the relative positions and widths of the peduncular columns, permitting the newly formed upper latus to articulate closely with, and partially overlie, both the scutum and tergum (see above). This brings the upper latus (ul) column (formerly t) to a central position on the side of the peduncle, where it is positioned in later scalpellomorphs. Formation of the carinolatus was accompanied by a similar lateral shift in the c2 column, such that it sat directly beneath the carinolatus. The loss of one scutal column, probably s2, left a single peduncular column directly beneath the scutum in stramentids. Finally, and at a later stage, the evolution of the rostrolatus resulted in the transfer of the scutal column to the rl (r).

Homologies between *A. redienbacheri* and stramentids can be identified as: (1) the c1 and r columns are the same; (2) the c2 column has evidently transferred to the carinolatus (cl); (3) the t column has transferred to the ul; and (4) one of the two scutal columns has been lost.

The transition to the plesiomorphic scalpellid condition, and the terminology of Newman & Ross (1998) involves transfer of the scutal column to the rl and development of an inframedian latus (Fig. 2F).

### Cladistic analysis of basal scalpellomorphs and stramentid relationships

#### Polarity determination

There is a consensus which extends back to the work of Withers (1928) that a number of features of *Eolepas, Archaeolepas* and stramentids are plesiomorphic among scalpellomorphs, most notably the small number of capitular plates (*Archaeolepas, Eolepas*: six — carina, rostrum, two scuta, two terga; stramentids: 10, with upper laterals and carinolaterals) and the robust eight columns of peduncular plates found in *Archaeolepas* and stramentids (Newman & Ross 1998; Young 2001). Indeed, most evolutionary scenarios place *Eolepas* at the base of the scalpellomorphs, and trace its origin back to the five-plated Carboniferous *Praclepas* (see Fig. 5; Newman 1979, 1987), usually interpreted as a lepadomorph. The progressive acquisition of additional capitular plates (upper laterals, carinolaterals, rostrolaterals, subrostra, subcarinae) is then interpreted as progressive evolution towards more derived scalpellomorphs (Fig. 5). The discovery of living cirripedes in which the capitulum consists of only eight plates (two scuta, two terga, carina, rostrum + two upper latera) was interpreted as evidence of ‘living fossils’ (Newman 1979). *Neolepas* and the three additional, closely related, genera which comprise the Neolepadinae are all found associated with hydrothermal vents — a source of supposed Mesozoic relicts (Newman 1979; Yamaguchi et al. 2004).

In the ontogeny of the scalpellomorph *Pollicipes* (Broch 1922), the primordial five plates (two scuta, two terga, carina) form first, then, successively, the rostrum, the upper laterals, and later the carinolaterals, rostrolaterals and subrostrum (Fig. 5). Paedomorphic evolution at various stages of this ontogenetic sequence could produce, for example, a lepadomorph morphology (five plates: two scuta, two terga, one carina), or a neolepadine (eight plates: rostrum, carina, two terga, two scuta, two upper latera). Newman’s (1979, fig. 5: 1987) model of thoracican evolution identified a succession of living and fossil taxa as corresponding to individual ontogenetic stages of *Pollicipes* (Fig. 5). Thus, the ontogeny of *Pollicipes* has been interpreted as recapitulating phylogeny.

However, this rather neat scenario presents a number of problems. The first of these is the possibility that recurring paedomorphic evolution has produced apparently plesiomorphic taxa, as has been widely demonstrated in diverse animal phyla (McNamara 1995). Because all scalpellomorphs appear to undergo a basically similar ontogeny, the likelihood that superficially plesiomorphic forms have repeatedly evolved is strong.

A problem with cirripedes is that the rather simple morphological structures do not readily permit cladistic testing of possible paedomorphic derivation, as can be achieved in vertebrates, for example.

The widely accepted model of thoracican cirripede evolution (Fig. 5) was challenged by the publication of the first substantial molecular phylogeny of the group (Pérez-Losada et al. 2008). In this, calanctids appear as basal to the scalpellomorph radiation, and lepadomorphs appear as sister group to the bulk of the group, plus some supposed verrucomorphs (*Neoverruca*). Lithotrysiids and pollicipedids are the sister group to the balanomorphs plus the verrucomorphs. Although there are some significant conflicts with the fossil record, the fundamental message of the molecular analysis is that it is probably incorrect to follow simplistic morphological scenarios of thoracican cirripede evolution strictly. Additionally, the molecular tree supports at least two paedomorphic pathways, the derived positions of the apparently plesiomorphic Neolepadinae...
and Lepadomorpha. Two hypotheses are proposed to test the position of basal scalpellomorphs.

**Hypothesis 1.** *Archaeolepas* is a basal calcareous thoracican, which shows the plesiomorphic condition of a six-plated capitulum and 10 columns of peduncular scales. Stramentids represent an offshoot from the main thoracican tree which develops the plesiomorphic eight-plated peduncle, but at a stage at which the upper latus and carinolatus had evolved, but prior to the rostrolatus.

**Hypothesis 2.** The condition in *Archaeolepas* and stramentids represents a secondary reversal, or two independent reversals, characterized by the loss of one lateral
plate (stramentids) and all laterals (Archaeolepas), and a reduction of peduncular plate columns to eight, presumably from a more derived scalpellomorph.

There are a number of ways of testing these alternatives, both of which are superficially quite plausible, suggested long ago by Withers (1928). Witness the peduncular plate reduction common in diverse scalpellids (Young 2001), which can reduce from eight columns to two (Newman & Ross 1998), and the loss of all lateral plates except the upper latus in Neolepadidae and Neoverruca.

Test 1. There appears to be something fundamental about the eight-plated arrangement of peduncular scales in scalpellomorphs, because the cl-l-rl, c-r columns match precisely the capitular plates which give them their names in eight-plated forms. The plates are also introduced in a consistent order (Newman & Ross 1998). Only exceptionally is there any further reduction. In a detailed review of peduncular plates by Young (2001), the eight-column condition was interpreted as plesiomorphic for scalpellomorphs.

Test 2. The stratigraphical order in which successive taxa and morphological innovations appear provides a test for phylogenetic hypotheses (Smith 1994). Archaeolepas first occurred in the Callovian (Withers 1928), and continued into the Trias. The relatively derived zeugmatolepadids (according to Hypothesis 1) appear slightly earlier, in the Bathonian (Withers 1928; 168 Ma). The stramentids appear significantly later, in the late Aptian (c. 125 Ma). There appears to be little stratigraphical support for either hypothesis; however, the Mesozoic fossil record of thoracicans can be seen as very incomplete and patchy; a diversity of scalpellids appear contemporaneously in the Aptian (Arcoscalpellum, Virgiscalpellum) and must have had a significantly older radiation unrepresented by the known fossil record. Cretiscalpellum, which is generally regarded as a calanticid, but can be interpreted as the sister taxon basal to the Scalpellidae, appears in the Trias (Gale 2014a).

Test 3. The secondary reductions in capitular and peduncular plates seen in derived scalpellomorphs are not inherently associated. Thus, neolepadids lose all laterals except the upper latus, but retain numerous and irregular columns of small peduncular plates. In contrast, scalpellids reduce the number of peduncular columns, but usually retain a full complement of lateral plates (Young 2001). The condition in Archaeolepas and stramentids, in which both laterals and peduncular columns are reduced, can therefore be reasonably interpreted as plesiomorphic. The consensus would therefore appear to support Hypothesis 1, and the polarity of characters in the list (Supplemental material) is determined accordingly.

Basal scalpellomorph relationships

A single tree (Fig. 6) was recovered from heuristic, unconstrained analysis (stepwise additions option random, branch swapping option TBR [tree bisection and reconnection]) of 12 characters in Ibla, Idioibla, Praelepas, Eolepas, Archaeolepas, Stramentum, Arcoscalpellum and Zeugmatolepas.

There is stepwise introduction of characters within basal thoracicans, in a stratigraphical order matching the cladogram (except Ibla). Thus, Praelepas (Late Carboniferous) is the most basal taxon with five primordial plates and a carina; Eolepas (Trias) acquired a rostrum, rhomboidal terga and a concavo–convex triangular scuta, and thus resembles later scalpellomorphs. Finally, Archaeolepas (mid-Jurassic) developed peduncular plates, and Stramentum (Cretaceous) acquired an upper latus and a carinolatus.

An abrupt change takes place in plate chemistry from forms with a phosphatic composition (Ibla, Praelepas, Eolepas) to those with a calcareous composition (Archaeolepas, Stramentum, scalpellids). Høeg et al. (1999) considered that such a change was so improbable that they excluded the possibility from their cladistic analysis. However, as pointed out by Buckeridge & Newman (2006), there is no doubt that Eolepas is morphologically similar to scalpelliforms, as confirmed here. The possibility that Eolepas independently evolved this morphology cannot be ruled out entirely, but if this were the case, we have no fossil evidence for the ancestry of calcite-shelled pedunculate thoracicans, which would be surprising, given the high preservation potential of their plates.

The phylogenetic analysis is only partly complete, because the study omitted numerous scalpellomorphs including the calanticids, which also possess extra lateral plates and have been shown by molecular analysis to be the sister group to the scalpellids (Pérez-Losada et al. 2008) and thus are part of the story. It appears that scalpellomorphs went through a stage in the Jurassic, represented by the zeugmatolepadids, in which they evolved numerous lateral plates, which were secondarily lost in the lineage leading to the scalpellids but retained in the pollicipedids. Confirmation of this will require considerable additional work beyond the scope of the present study.

Cladistic analysis of the Stramentidae

A set of 25 characters (Supplemental material) was analysed using PAUP (heuristic unconstrained analysis, stepwise additions option random, branch swapping option TBR) and a single consensus tree was generated (Fig. 7), using Archaeolepas and Eolepas as outgroups. Stramentidae form a well-supported clade (100% bootstrap), but within this clade the relationships between Loriculinae (74%, Metaloriculina gen. nov., Loriculina), Leweslepas gen. nov., Angulotergum, S. pulchellum and Parastramentum gen. nov. + S. elegans (89%) are not resolved and form a polytomy. This is caused by numerous character reversals and parallels within Stramentidae, such as in the position of the scutal umbo, a character that has changed from an apical...
Palaeobiology of stramentids

The first stramentid ever described (see Fig. 19B) was attached to an ammonite (G. B. Sowerby Jr 1843; Darwin 1851a), and ever since then stramentids have most often been found attached to the shells of ammonites (e.g. Collins 1986; Ifrim et al. 2011). Preservation of stramentids by ammonite bioimmuration (overgrowth) has been recorded from the Aptian of the Caucasus (Drushchits & Zevina 1969) and the Turonian of Germany (Wittler 1996), unequivocal evidence for in-life attachment. Hauschke et al. (2011) used the attachment of a Stramentum to the orthoconic baculitid ammonite Sciponoceras, and the orientation of its occludent margin towards the apertural end of the shell, as evidence for the horizontal life orientation of those ammonites. Material figured here from the Santonian Niobrara Chalk of Kansas shows abundant Stramentum attached to the flanks of large baculitid ammonites (see below), although it is not possible to be certain that attachment happened during life.

However, Stramentum elegans Hattin, 1977 from the middle Turonian Fairport Member of Kansas was exclusively benthic in habitat, attaching most commonly to large, living inoceramid bivalves, more rarely to other epi- zoans on these shells, and very rarely to ammonite shells lying on the sea floor (Hattin & Hirt 1991). Without evidence from bioimmuration, it is not possible to tell whether attachment took place in life, onto dead, floating shells, or onto sunken shells of dead ammonites on the seafloor.

Systematic palaeontology

Superorder Thoracica Darwin, 1851b
Order Scalpelliformes Buckeridge & Newman, 2006

Remarks. The group is technically paraphyletic, because it does not include the common ancestor and all descendants, which must include the Sessilia (Gale 2014b; Gale & Sørensen 2014), but it is useful and is therefore retained here.

Family Eolepadidae Buckeridge, 1983


There are a number of problems with this classification. Firstly, Høeg et al. (1999) claimed that the valves of Eolepas were made of calcium phosphate (confirmed here; see above), and, more contentiously, proposed that the genus lacked a rostrum. They therefore placed Eolepas in a separate clade, basal to all other thoracicans, together with Ibla. Buckeridge & Newman (2006) challenged both issues, suggesting that the valves of Eolepas might not be completely phosphatic, or were secondarily phosphatized, and that a rostrum was in fact present. On this basis they left the family in the Scalpelliformes.

Pérez-Losada et al. (2008) demonstrated on the basis of molecular phylogeny that neolepadids (Neolepas, Ashinklelapas, Leucolepas, Volcanolepas) were the sister group to Neoverruca spp., which in turn was the sister group to Scalpellidae. Gale (2014b) confirmed the close relationship between Neolepadidae and Neoverruca from morphological evidence. This effectively removed the clade from the ancestry of the scalpellomorphs, and falsified the hypothesis that Neolepas represents a transitional form between Archaeolepas, which lacks lateral plates, and later scalpellomorphs, which have a full complement of laterals (Newman 1979).

In conclusion, Eolepadidae is considered to be paraphyletic, including taxa which can be considered morphologically to be the sister group to the scalpellomorphs (Eolepas), but which possess a phosphatic skeleton, as well as taxa which represent basal, calcareous scalpellomorphs, such as Archaeolepas, with a calcitic composition and peduncular plates. Therefore, only Eolepas is retained in Eolepadidae.

**Clade Thoracicalcarea nov.**

**Diagnosis.** Thoracica in which the shell plates are composed of calcite.

**Remarks.** The mineralogical change from phosphate to carbonate which took place between Eolepas and Archaeolepas (Fig. 6) is a fundamental event in the history of the Thoracica, and marks the base of a monophyletic clade including all scalpellomorphs except Eolepas, plus Sessilia. The rank of this clade within the broad classification must await further study.

**Genus Archaeolepas** von Zittel, 1885

**Type species.** Pollicipes redtenbacheri Oppel, 1862, by subsequent designation of Withers (1928, p. 83). Tithonian, Germany.

**Referred species.** Pollicipes royeri de Loriol in de Loriol et al., 1872, Kimmeridgian, Haute Marne, France.

**Emended diagnosis.** Calcareous scalpellomorphs which lack lateral plates and have a peduncle consisting of 14 columns of nearly even breadth, composed of strongly imbricating plates. Peduncle and capitulum of approximately even height, carina less than half the height of tergum. Tergum and scutum smooth, convex.

**Remarks.** The original material of Oppel (1862) and von Zittel (1885) is refigured here (Fig. 3A–D), and provides little information to further the descriptions of Withers (1928). However, there is now more material available in private collections from the Tithonian plattenkalk of southern Germany, which will provide the basis for eventual redescription of the species. Archaeolepas can be
readily distinguished from *Loriolepas* gen. nov. by the robust form of the peduncle, with 10 columns of large plates, whereas the new genus has more than 20 columns of much smaller plates. Additionally, the low capitulum and carina, which is less than half the height of the tergum, are distinctive.

**Genus Loriolepas** gen. nov.

**Derivation of name.** For the great Swiss palaeontologist and zoologist, Perceval de Loriol (1828—1908).

**Type species.** *Pollicipes suprajurensis* de Loriol in de Loriol & Pellat, 1867.

**Referred species.** *Archaeolepas decorata* Harbort, 1905, from the Valanginian of Musingen, Bückeburg, Germany (Fig. 4B, C, F, G). *Pollicipes planulatus* Morris, 1845.

**Diagnosis.** Scalpelliforms which lack lateral plates, and possess a capitulum which is less than half the height of the peduncle. Peduncular plates small, polygonal, set in 20¢ columns. Carina two-thirds the height of tergum, strongly incurved towards tergum. Tergum possesses sharply demarcated, flat-topped apicobasal ridge which forms a basal margin.

**Remarks.** *Loriolepas* gen. nov. differs significantly from *Archaeolepas*, from which it is presumably descended, in the smaller peduncular plates set in more numerous columns (Fig. 4A—C), the tall incurved carina, and the presence of apicobasal ridges on terga and scuta (Fig. 4D—G). The new genus gave rise to the distinctive Late Cretaceous family Myolepadidae Gale in Gale & Sørensen, 2015, characterized by the presence of rostro- and tergocutal depressor muscles, and locally abundant in nearshore Late Cretaceous environments (Gale & Sørensen 2015).

**Family Stramentidae** Withers, 1920

**Diagnosis.** Oval, laterally compressed calcareous thoracicans which possess a carinolatus, an upper latus and a peduncle which is covered by eight columns of strongly imbricating plates.

**Remarks.** The monophyly of this family is strongly supported by the cladistic analysis (Fig. 6). The terminology used here follows Hattin (1977) (see Fig. 8). It should be noted that the term ‘rostral slip’ is replaced by ‘rostral articulation surface’, and that a numerical value is used for the position of the scutal umbo, with, for example, an apical position designated 0/10, a central position 5/10 and a basal position 10/10. The concept of capitular angle is introduced here, which is the angle subtended by the axis of the middle peduncular column (upper latus column) to the base of the capitulum. Thus, *Leweslepas* gen. nov., in which the boundary between the capitulum and peduncle is transverse, has a low capitular angle (95—100°), whereas species such as *Stramentum pulchellum* and *S. inconstans*, in which the boundary slants, have high capitular angles (110—125°).

**Subfamily Loriculinae** subfam. nov.

**Diagnosis.** Stramentids in which the carinolatus and tergum are arranged transversely, and their contact is subparallel to acutely angled; tergum broad, flat, rectangular to subtriangular in outline; contact between peduncular plates of carinolatus and upper latus columns flat, with no interdigitation. Plates of rostral column of peduncle V-shaped, with inner median vertical groove.


**Remarks.** The discovery of complete articulated specimens of *Loriculina ifrimae* sp. nov. (Fig. 10) and *Metaloriculina stramentoides* gen. et sp. nov. (Figs 9E, 12) in the Coniacian of Mexico, and abundant isolated valves of *Metaloriculina norvicensis* gen. et sp. nov. in the upper Campanian of Norfolk, UK, permits definition and detailed description of the subfamily. The most distinctive features are the transversely arranged tergum and carinolatus, the rectangular to subtriangular tergum, and the flat contact between peduncular plates of the carinolatus and upper latus columns (Fig. 9). *Metaloriculina* gen. nov., also from the Coniacian of Mexico, shares these characters, but also possesses a centrally positioned scutal umbo. The position of this feature has been previously used to separate *Loriculina* (apical) and *Stramentum* (subapical) (see Withers 1935; Hattin 1977; Hauschke 1994). Furthermore, the discovery of articulated stramentids in the Cenomanian of the UK which possess an apical scutal umbo, but are otherwise similar to *Stramentum* (e.g. acutely angled carinolatus—tergum contact, strongly interdigitating carinolatus—upper latus peduncular plates) necessitates change to the definition of the genus *Loriculina*. A simple solution, adopted here, is to divide the Stramentidae into two subfamilies, *Loriculinae* nov. and *Stramenti- nae*, on the basis of these consistent characters. The development of a subapical umbo probably occurred three times in the evolution of Stramentidae.

A further interesting discovery is that the peduncular plates of the rostral column of *Metaloriculina norvicensis* gen. et sp. nov., from the upper Campanian of Norfolk, UK, are highly distinctive: they are V-shaped, and on the interior possess an apicobasal median groove which presumably carried a soft structure such as a ligament in life (Figs 11, 13). Similar plates are visible in the holotype of *Loriculina ifrimae* sp. nov., and the presence of these plates adds to the unique morphology of *Loriculinae*.
Figure 8. Terminology of the stramentid skeleton (after Hattin 1977, text-fig. 2). Note that the term ‘rostral slip’ is in this paper replaced with ‘rostral articulation surface’. The peduncular plate columns are rostral (1), scutal (2), upper latus (3), carinolatus (4) and carinal (5).
the upper Campanian of Norfolk provides additional information about the peduncular construction of stramentids. Although articulated individuals of stramentids are a major source of morphological information, they are almost invariably flattened laterally, and it is not usually possible to see details of the articulations of the plates (Hattin 1977). The isolated plates can be readily assigned to both taxa, and to individual plate columns, with reference to articulated material. Thus, they provide information about articulation patterns, and, because the plates are three dimensional, allow accurate reconstruction of the cross-sectional shape of stramentids for the first time. Metaloriculina gen. nov. possessed processes for articulation on the upper latus column (Fig. 11), inserting under the carinolateral and scutal columns, respectively, absent in Parastramentum gen. nov. and Stramentum (Fig. 27). Additionally, the material demonstrates that the rostral side of the peduncle cross section in Metaloriculina gen. nov. was much broader than the carinal side, with strongly convex plates of the scutal column (see the description of M. norvicensis gen. et sp. nov. below for details). In contrast, Parastramentum gen. nov. was symmetrically oval in cross section (see Fig. 28).

Blastolepas is provisionally referred to Loriculinae gen. nov., on the basis of the oblique contact between the carinolatus and the tergum.

Genus **Blastolepas** Drushchits & Zevina, 1969

**Type species.** Blastolepas orlovi Drushchits & Zevina, 1969, upper Aptian, Caucasus.

**Remarks.** The drawings of Blastolepas orlovi provided by Drushchits & Zevina (1969) are curious in a number of ways, probably because of the poor preservation of the material which made its interpretation difficult. However, the highly irregular arrangement of the peduncular plates (Drushchits & Zevina 1969, fig. 2) is not supported by the photographs (e.g. Drushchits & Zevina 1969, pl. 11, fig. 16), which show a regular arrangement of eight columns as in Stramentidae. An equilaterally triangular upper latus is clearly present (Drushchits & Zevina 1969, pl. 11, figs 3, 6, 16), and a transversely elongated carinolatus sits beneath the tergum. The scutum has a convex occludent margin (Drushchits & Zevina 1969, pl. 11, fig. 16), and I suspect that the ‘subcarina’ is a displaced plate from the carinal column. The reconstruction provided here (Fig. 9D) is admittedly based on very limited evidence, but it interestingly shows a number of features in common with the new reconstruction of Loriculina (see below).

Blastolepas is provisionally interpreted as a stramentid in which there is a small rostrum, and the scutum has a convex occludent margin. The upper latus is symmetrically triangular, but the carinolatus is broad and low, tapering towards the upper latus. The tergum is rhombic and relatively tall, and contacts both the upper latus and the scutum on its scutal margin. A tall carina contacts both the carinolatus and the tergum.

The general construction of the capitulum is similar to that in Loriculina ifrimae sp. nov. (see below) in the shape and size of the rostrum and scutum; the transverse form of the carinolatus, with a long near-horizontal contact with the tergum; the contact between the carinolatus, tergum and upper latus; and the tall carina which articulates both with the carinolatus and tergum. A difference is the attitude of the capitulum to the axis of the peduncle, which is about 90°, and this is reflected in the symmetry of the upper latus in B. orlovi. In Loriculina, the base of the capitulum is slanted at 50–60° to the axis of the peduncle, and the upper latus is asymmetrical. The tergum is very different; it is rhombic and tall in B. orlovi, but low, rectangular and transversely elongate in L. ifrimae sp. nov.

The tall tergum is reminiscent of the condition in Archaeolepas, and can thus be interpreted as plesiomorphic with respect to the derived state in Loriculina. Blastolepas is therefore identified as the most basal stramentid, which provides important clues to both the origin of the family and the evolution of lateral plates in scalpellomorphs (see above).

The broad, low carinolatus in Blastolepas resembles a peduncular plate in form, and it seems feasible that this is how the plate originally evolved, by transfer of the uppermost plate of the (originally) tergal column of peduncular plates into the capitulum; the peduncular column then became the carinolatus column of all subsequent scalpellomorphs (see Young 2001). The highly derived stramentids probably separated from the mainstream of scalpellomorph evolution shortly after the carinolatus had formed, and the low, transverse form of the carinolatus in Blastolepas and Loriculina retains the plesiomorphic condition. The origin of the stramentids thus predated the evolution of a rostrolatus, presumably by an equivalent plate transfer from the peduncle. This stage of evolution is unfortunately not yet represented by fossil material.

Genus **Loriculina** Dames, 1885

**Type species.** Loriculina noettingi Dames, 1885, by subsequent designation of Withers (1935, p. 303).

**Diagnosis.** Loriculinae in which the scutal umbo is apical in position; the scutum is tall, triangular and inclined towards the tergum; the scutum is thin, and lacks an internal shelf above the scutal adductor; the occludent margin is gently convex, and has a narrow, depressed margin; the margin in contact with the upper latus is strongly concave.

**Age.** Late Turonian–early Campanian.

**Remarks.** Until very recently, Loriculina was a rare and somewhat enigmatic genus, the understanding of which was based largely on two, small, incomplete individuals — the
The types of *L. noetlingi* Dames, 1885 from the upper Santonian of Lebanon, and *L. laevissima* (von Zittel, 1885) from the lower Campanian of Westphalia, Germany. Withers (1935) referred isolated valves from the Turonian to the former species, and also placed *Loricula acuminata* Darwin, 1851a in *Loriculina*. This species is known only from an isolated scutum, probably from the Cenomanian of Stoke Ferry, Norfolk, and which was subsequently lost (Withers 1935).

The types of *L. laevissima* and *L. noetlingi* are both well preserved on the scutal–rostral side, but the carinolatus and tergum are incomplete, and the carina is completely missing (Fig. 9B, C, F). Withers (1935), in his major revision, described neither the tergum nor the carinolatus in these type specimens, although he somehow identified isolated valves from the English Chalk as terga of *L. laevissima* (Withers 1935, pl. 40, figs 8, 9, 12, 13). A cast of reasonable quality of the holotype of *L. laevissima* in the NHMUK collections is figured here as a drawing (Fig. 9B), and shows clearly that the tergum is transversely quite broad, and is situated above the carinolatus; they have a straight contact, subparallel with the cl column of peduncular scales, reminiscent of *Blastolepas* (Fig. 9D; see above) and quite different from the condition in *Stramentum*. The situation is similar in the type of *L. noetlingi*, but only scraps of the tergum and carinolatus remain. However, the shape and

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**Figure 9.** Drawings and photographs of Loriculinae subfam. nov. A, *Loricula ifrimae* sp. nov., based on the holotype (see Figure 10B), Lower Coniacian, Yellow Limestone Member, Carranza, northern Coahuila, Mexico; attached to ammonite *Peroniceras*; CPC-159. B, *Loricula laevissima* (von Zittel, 1885), drawing of holotype (original of *Loricula laevissima* von Zittel, 1885, fig. 4), Oberer Kreidemergel, Dülmen, Westphalia, Germany, lower Campanian; Bayerische Staatsammlung für Paläontologie und historische Geologie, München. C, F, *Loricula noetlingi* Dames, 1885, holotype (original of Dames, 1885, fig. 2), Fish Bed, Sahel Alma, Lebanon, upper Santonian; Museum für Naturkunde, Berlin. D, reconstruction of *Blastolepas orlovi* Drushlvtis & Zevina, 1969, Aptian, Caucasus. E, *Metaloricula stramentoides* gen. et sp. nov., drawing of holotype shown in Figure 12C; Lower Coniacian, Yellow Limestone Member, Carranza, northern Coahuila, Mexico; all attached to ammonite *Peroniceras*; CPC-159. Scale bars $= 5 \text{ mm}$. 

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orientation of the carinolatus and tergum remained unknown, as did the carina, making Withers’s identification of isolated terga appear to be rather ambitious.

**Description.** The complete form of *Loriculina* is now known from numerous specimens from the Lower Coniacian of Mexico, here described as *L. ifrimae* sp. nov. (Figs 9A, 10). These were figured by Ifrim et al. (2011, figs 5/5, 6) as *Stramentum pulchellum*, but the specimens have apical scutal umbones and the same transversely oriented junction between the carinolatus and overlying tergum as seen in the type of *L. laevisima*, and

**Figure 10.** *Loriculina ifrimae* sp. nov., Lower Coniacian, Yellow Limestone Member, Carranza, northern Coahuila, Mexico; all attached to ammonite *Peroniceras tridorsatum*, CPC-159 (see Ifrim et al. 2011, fig. 4). **A, C, D,** paratypes; **B,** holotype (original of Ifrim et al. 2011, fig. 5/6, as *Stramentum pulchellum*). See also Figure 9A. Note particularly the transversely arranged, rectangular tergum and the abutting peduncular plates of the carinolatus and upper latus columns. Scale bars = 2 mm.
Remarks. Withers (1935) thought that the two known articulated specimens of *Loriculina* were young individuals, presumably because the terga he identified as belonging to the genus from the English Chalk were large. The new material from Mexico is also small, and to date the genus is not known to have exceeded a maximum height of 2 cm.

The new description of the morphology of *Loriculina* makes it possible to reassess the isolated valves referred to the genus by Withers (1935, pl. 40), with the following conclusions:

1. The robust scuta with apical umbones and a shelf above the adductor scar which Withers referred to *L. acuminata* (Withers 1935, pl. 40, fig. 1; after Darwin 1851a, pl. 3, fig. 6a, b) and *L. laevissima* (Withers 1935, pl. 40, figs 3–5) are quite unlike the delicate scuta of *Loriculina*, and also lack the depressed occludent margin of that genus. They are placed in the stramentine genus *Leweslepas* gen. nov., which has apical scutal umbones and a robust construction.

2. The delicate scuta from the Turonian chalk of ‘Alton’ (actually from Brydone’s (1912) Pit no. 125 at Foxfield, Hampshire), identified as *L. laevissima* by Withers (1935) are correctly referred to *Loriculina*. The specific identification appears to be uncertain, and they are here identified as *Loriculina* sp. The valves figured as terga (Withers 1935, pl. 40, figs 8, 9) are terga of *Parastramentum* gen. nov. (see below).

3. The large triangular concavo–convex valves from the lower Campanian Chalk of East Harnham (Withers 1935, pl. 40, fig. 13) and the Sussex coast (Withers 1935, pl. 40, fig. 12) identified as terga of *L. laevissima* cannot belong to *Loriculina*, because the new material of *L. ifrimae* sp. nov. demonstrates that the terga of the genus are flat and rectangular. East Harnham has also yielded three similarly large, rhombic and highly distinctive scuta, one of which is the type of *Stramentum expansum* (see Withers 1911), here placed in *Parastramentum* gen. nov. The comparably large size of the scuta and terga, the distinctive sculpture of clustered growth lines with a faint radial sculpture, and the similarity of the terga to those of *Parastramentum* gen. nov. make it likely that they also belong to *P. expansum*. This is confirmed by the association of terga and scuta of equivalent types from the Campanian Chalk of Norwich, here described as *Parastramentum peakei* gen. et sp. nov.

*Loriculina laevissima* (von Zittel, 1885)

(Fig. 9B)

1885 *Loricula laevissima* von Zittel: 589, fig. 4.
1885 *Loricula laevissima* Zittel; Dames: 155, fig. 3.
1935 *Loricula laevissima* (Zittel); Withers: 305, pl. 40, fig. 2 only.

Diagnosis. *Loriculina* in which the scutum is relatively low, with the angle between the basal and upper lateral

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**Figure 11.** Peduncular construction in *Loriculinae* subfam. nov., based on isolated plates of *Metaloriculina norvicensis* gen. et sp. nov. from the *Blemnithella mucronata* Zone, Newfound Farm Pit, Cringleford, Norwich, Norfolk, UK (Fig. 13), and articulated specimens of *M. stramentoides* gen. et sp. nov. from Mexico (Fig. 12). The lower drawing shows a cross-section of the peduncle.
margins of the scutum obtuse (120°) and straight; the ratio between the length of the basal margin and the height is low (1.3); the basal margin of the upper latus contacts a single peduncular plate.

**Type.** The unique holotype figured by von Zittel (1885) and Withers (1935) is from the Oberer Kreidemergel of Dülmen, Westphalia, Germany. According to Kennedy & Kaplan (1989), the Dülmen localities are lower Campanian, *granulataquadrata* and *quadrata/lingua* zones (*sensu germanico*). Bayerische Staatssammlung für Paläontologie und historische Geologie, München (see Withers 1935). A cast of the specimen is NHMUK In. 59713.

*Loriculina noetlingi* Dames, 1885
(Fig. 9C, F)

1885 *Loriculina noetlingi* Dames; 152, fig. 4.
1935 *Loriculina noetlingi* Dames; Withers: 308, pl. 40, fig. 14.

**Diagnosis.** *Loriculina* in which the scutum is upright, the angle between the basal and upper lateral margin is relatively acute (100°), and the ratio between the length of the...
Figure 13. Metaloriculina norvicensis gen. et sp. nov., lower Belemnella mucronata Zone, Newfound Farm Pit, Cringleford, Norwich, Norfolk, UK. A, peduncular plate from upper latus column, NHMUK IC 1223. B, E, carinolatera, external view; B, NHMUK IC 1224; E, NHMUK IC 1226 (holotype). C, D, peduncular plate from scutal column in lateral and apical views, NHMUK IC 1225. F, G, peduncular plate from rostral column in external and internal views, NHMUK IC 1227. H, peduncular plate of lower rostral column, NHMUK IC 1228. I, K, peduncular plates from carinolatus column, NHMUK IC 1229, 1231. J, L, peduncular plates from carinal column, NHMUK IC 1230, 1232. Scale bars = 0.5 mm.
basal margin and the height is high (1.7); the basal margin of the upper latus contacts two peduncular plates.

**Type.** The unique holotype has been found from the Fish Bed at Sahel Alma, Lebanon, which has been dated as late Santonian on the basis of planktic foraminifera (Ejel & Dubertret 1966). Reproduced here (Fig. 9F) is a recent image of the specimen from the Museum für Naturkunde, Berlin, taken by the late Martin Whyte, which shows that it has suffered damage since 1935.

**Remarks.** *Loriculina noettingi* is distinguished from its congeners by the lower scutum, and the broader upper latus column of peduncular plates.

*Loriculina ifrimae* sp. nov.  
(Figs 9A, 10)

p. 2011 *Stramentum pulchellum* (Sowerby); Ifrim et al.: figs 5/5, 6 only.

**Derivation of name.** For my friend Christina Ifrim, who found and figured the type specimens.

**Diagnosis.** *Loriculina* in which the scutum is low; the angle between the basal margin and that with the upper latus is obtuse (120°) and the ratio between the length of the basal margin and the height is low (1.1). The contact between the scutum and the upper latus is markedly curved. The basal margin of the upper latus contacts three peduncular plates.

**Type specimens.** The holotype is the individual figured by Ifrim et al. (2011, fig. 5/6, refigured here (Fig. 10B); the other figured specimens are paratypes. All are attached to an ammonite, *Peroniceras*, from the lower Coniacian, Yellow Limestone Member, Carranza Quarry, Coahuila, Mexico. CPC-159.

**Description.** Fifteen specimens, in various states of completeness, from piles of valves to complete, articulated individuals are present on the flank of the *Peroniceras*. The body is oval with nearly symmetrical taper to the apex of the capitulum and the attachment site, and the long axis is approximately twice the maximum width, which falls at the level of the rostrum. The capitular angle between the base of the capitulum and the long axis of the peduncle is acute (c. 50°, as compared to 70° in *Stramentum elegans* – see below), and the occludent margin is slightly convex; the tergal and scutum each make up 50% of the occludent margin. The apex of the capitulum is coincident with that of the tergum, and is positioned slightly to the tergal side of the long axis of the peduncle. The arrangement, shape and orientation of the capitular plates is highly distinctive; the apices of the scutum and upper latus are close together, and both are inclined markedly towards the tergum. Secondly, and most distinctively, the tergum lies above the carinolatus, and their contact is subparallel with the base of the capitulum.

The scutum is triangular, and strongly inclined towards the tergum. The upper lateral margin is concave, the occludent margin gently convex. The interior of the scutum is smooth and concave, without a shelf above the scutal adductor. The carina is tall and narrow and the apex lies close to that of the tergum. The tergum is rectangular; the long occludent margin is parallel with the carinal lateral margin, and the short upper lateral margin is set at right angles to these. The plate is three times as broad as high, and the umbo is positioned centrally at the summit of a short carinal margin. The growth lines are parallel with the carinolateral margin, and inflect sharply to run parallel with the upper lateral margin. The carinolatus is triangular, but the margin which contacts the upper latus is truncated. The acutely pointed apex is situated at the point of contact with the carina and tergum. The basal and tergal margins taper gradually towards the upper latus. The growth lines run subparallel with the basal margin, but inflect towards the apex in the central portion of the plate. The upper latus is triangular and the scutal margin is convex; the tergal margin is straight.

The peduncle has a morphology typical of *Loriculina* (see above), in which the contact between plates of the carinolatus and upper latus columns is flat or slightly concavo—convex and opposed, not interpenetrant. The plates of the rostral column are V shaped with rounded wings, which diverge apically. Plates of the carinal column are rectangular and gently convex.

**Remarks.** *Loriculina ifrimae* sp. nov. is closest to *L. laevissima*, from which it differs in possession of a strongly curved margin between the scutum and upper latus (straight in *L. laevissima*), and the proportionately broader and taller peduncular plates of the upper latus column.

*Loriculina* sp.

vp. 1935 *Loriculina laevissima* (Dames); Withers: pl. 40, figs 6, 7 only.

**Material.** Three fragmentary scuta from the *Holaster platus* Zone, upper Turonian, Froxfield, Hampshire. Pit No. 125 of Brydone (1912), close to junction of Barnet Side Lane and King’s Lane, Froxfield, 5 km north-west of Petersfield, Hampshire. SM 704275. NHMUK In. 32485, 32486.

**Remarks.** The only specimens figured by Withers (1935) from the English Chalk as *Loriculina* which can be referred to the revised concept of the genus are two fragmentary scuta in the NHMUK collections, and a further fragment in the SM collections. These are smooth, thin and concavo—convex, with convex occludent margins, and a narrow depressed rim parallel with the occludent margin. They cannot be assigned to any species at present. Valves referred to
as terga of *L. laevissima* from the same locality are actually terga of *Parastramentum* gen. nov. (see below).

**Loriculina colombiana** (Royo y Gomez, 1941)

1941 *Loricula colombiana* Royo y Gomez: 210, figs 1–3.

Type specimens. The material figured by Royo y Gomez (1941); the individual from the Albion of Calera de La Frontera, Colombia, is here designated lectotype. Current whereabouts unknown.

Remarks. The illustrations of Royo y Gomez (1941), particularly his figure 3, show a stramentid with an apparent apical scutal umbo, and a transversely arranged tergum and carinolatus, which suggest affinity with *Loriculina*. However, the peduncular plates are much more like those of *Stramentum*, in that there is extensive interdigitation between the plates of the upper latus and carinolatus columns, rather than the opposed plates seen in *Loricula*. In the end, the illustrations are not adequate enough to be sure of the generic affinity.

**Genus Metaloriculina** gen. nov.

Type species. *Metaloriculina stramentoides* sp. nov.

Referred species. *Metaloriculina novicensis* sp. nov. from the upper Campanian of Norfolk, UK.

Derivation of name. From the Greek word *meta*, meaning beyond, with reference to the differences which separate the genus from *Loriculina*.

Diagnosis. Loriculine in which the apical scutal umbo is positioned centrally to subcentrally (5–6/10), and the rhombic scutum has a pointed apex.

Remarks. Among the stramentids adherent to *Peroniceras tridorsatum* from Carranza Quarry, Coahuila, Mexico, are some six small individuals which have capitel valves of similar morphology to those of *Loriculina* (transverse, rectangular terga, triangular, transversely arranged carinolatera), but which possess centrally positioned scutal umbones like those in the stramentines *Stramentum* and *Parastramentum* gen. nov., yet have a tall, acuminate apical process on the scutum. Isolated valves from the Upper Campanian of Norwich, Norfolk, UK, are referred to the same genus, as the tergal morphology is typical of Loriculinae nov. but the associated scuta have a central umbo.

**Metaloriculina stramentoides** sp. nov.

(Figs 9E, 12)

p. 2011 *Stramentum pulchellum* (Sowerby); Ifrim et al.: fig. 5/5 only.

**Types.** Holotype is the individual figured by Ifrim et al. (2011, fig. 5/4), refigured here (fig. 12C). The other individuals figured here (Fig. 12A, B, D) are paratypes. Attached to *Peroniceras tridorsatum*, lower Coniacian, Yellow Limestone Member, Carranza Quarry, Coahuila, Mexico. CPC-159.

Derivation of name. With reference to the *Stramentum*-like scutum of the genus.

Diagnosis. Metaloriculina in which the apical portion of the scutum is tall and pointed.

Description. The body form is asymmetrically oval, the capitular angle moderately high (120°) and the occludent margin is convex. All plates display prominent growth lines. The tergum and carinolatus are flat and transversely elongated, and the margin between these plates is acutely angled to the base of the capitulum. The tergum is trapezoidal in outline with a straight carinolateral margin and a gently convex occludent margin. The growth lines run parallel to the upper lateral margin across most of the surface of the plate, and inflect apically close to the carinolateral margin. The carinolatus is triangular with a long basal margin, and the narrow, tall carina articulates with the straight carinal margin of the carinolatus. The upper latus is triangular, slightly broader than high, the scutal margin is slightly convex, and the tergal margin is slightly concave. The scutum is nearly rhombic in outline, and has a large umbonal angle (150–170°) and a tall, pointed apex with an acute apical angle (35–40°). The umbo is central to subcentral (5–6/10). The basilateral angle is openly rounded and quite obtuse (110°), the basal angle acute (60°).

The peduncular plates of the three lateral columns are four times broader than high, and those of the upper latus column are strongly crescentic. The plates of the scutum and upper latus columns interdigitate strongly, and the plates of the upper latus and carinolatus columns have a flat or gently concavo–convex contact and oppose. Plates of the carinal column are rectangular and slightly asymmetrical. No rostral column plates are visible on any individual.

Remarks. The loriculine affinities of this species are shown by the shape and arrangement of the tergum and carinolatus, the articulation of the peduncular columns (opposing, flat carinolatus–upper latus column contact), and the form of the carinal column.

**Metaloriculina novicensis** sp. nov.

(Figs 13, 14—K)

Types. The holotype is the carinolatus shown in Figure 13E, NHMUK IC 1226. Other figured specimens are paratypes (NHMUK IC 1223–5, 1227–1232).

Material. Three carinolatera, one upper latus, three scuta, 25 peduncular plates, from sample levels Cr1–3,
Figure 14. Barnacles from the Upper Cretaceous. A–D, Zeugmatolepas cretae (Steenstrup, 1839); A, B, scutum in external (A) and internal (B) views, upper Campanian, *Belemnitella mucronata* Zone, Weybourne Chalk, Keswick, Norwich, UK, NHMUK IC 1233; C, D, scutum, holotype of *Stramentum biplicatum* Jagt & Collins, 1989, Zeven Wegen Chalk Member, upper Campanian, CPL Quarry, Haccourt, Belgium, original of Jagt & Collins (1989, fig. 4J, K), NHMUK In. 63637. E, Stramentidae?, scutum, external aspect, NHMUK IC 1235, Upper Campanian, *Belemnitella mucronata* Zone, Newfound Farm Pit, Cringleford, Norwich, Norfolk, UK. F, M, *Parastramentum peakei* gen. et sp. nov.; F, large tergum in external aspect, NHMUK IC 1234; M, holotype scutum in external view, NHMUK IC 1238, Upper Campanian, *Belemnitella mucronata* Zone, Newfound Farm Pit, Cringleford, Norwich, Norfolk, UK. G, H, *Parastramentum brydonei* gen. et sp. nov., holotype tergum in external (G) and internal (H) views, Upper Turonian, *Holaster planus* Zone, Pit no. 125 of Brydone (1912), Froxfield, Hampshire, UK, SM 76166. I–K, *Metaloriculina norvicensis* gen. et sp. nov., scuta, *Belemnitella mucronata* Zone, Newfound Farm Pit, Cringleford, Norwich, Norfolk, UK. I, J, external (I) and internal (J) views of paratype scutum, NHMUK IC 1236; K, paratype scutum, IC 1237. N–P, *Parastramentum expansum* (Withers, 1911), *Actinocamax quadratus* Zone (lower Campanian), East Harnham, Salisbury, Wiltshire, UK; N, O, scuta; O, holotype and original of Withers’ (1911, fig. 8a, b), NHMUK In. 13812; N, NHMUK In. 27275; P, tergum figured as *Loriculina laevissima* (von Zittel, 1885) by Withers (1935, pl. 40, fig. 13), NHMUK In. 30527. L, *Parastramentum* sp., tergum figured as *Loriculina laevissima* (von Zittel) by Withers (1935, pl. 40, fig. 12), *Oeffoster ptilula* Zone (lower Campanian) coast of Sussex, UK, NHMUK In. 32491. Scale bars: A–E, G, H, L–P = 1 mm; F, I–K = 0.5 mm.
Cringeford Newfound Farm Pit, Norwich, Norfolk, UK; peduncular plates from Keswick, Norwich. *Echinocorys conica* level, *Belenitella mucronata* Zone, upper Campanian (Wood 1988). The identification of plates is made with reference to articulated material of *M. stramentoides* sp. nov. from Mexico.

**Derivation of name.** After the Roman name for the city of Norwich, *Norvica*, where the type material was collected.

**Diagnosis.** *Metaloriculina* in which the apex of the scutum is short and not pointed; there is a discrete tergal surface on the carinolatus.

**Description.** The carinolatus (Fig. 13B, E) is flat, sub-triangular and elongated, with straight margins (2.5 x longer than high). The tergal margin is long and straight, and is set at right angles to the short upper marginal margin. The carinal margin is straight and acutely angled (25°) to the tergal margin. The growth lines run parallel with the basal margin on the lower part of the plate, then deflect up to the tergal margin, parallel with the upper lateral margin. The upper latus is triangular, as tall as broad, and the scutal margin is convex; the tergal margin is slightly concave. The scutum (Fig. 141 – K) is rhombic, with an acute rostral angle (60°), a strongly obtuse umbonal angle (150°) and an obtuse basilateral angle (115°). The umbo is approximately central in position (4–5/10).

All columns of peduncular plates are represented in the material, and can be confidently referred to their correct positions with reference to articulated material of *M. stramentoides* sp. nov. The arrangement of the plates is illustrated in Figure 11. Plates of the rostral column are highly distinctive, V shaped and flat, with apically divergent wing-like processes, and on the interior surface bear a vertical median groove (Fig. 13F, G). The growth lines deflect downwards on the lateral tips of the wings. The most apically positioned plates are symmetrical, the wings diverge at a relatively acute angle (60°) and the groove is partially covered by two lateral processes. In plates from lower down the column (Fig. 13H), the angle between the wings is more obtuse (70–75°), the wings are markedly asymmetrical and the median groove is open.

Plates of the scutal column (Fig. 13C, D) are concavo-convex and asymmetrically crescentic, with upturned lateral processes of different lengths. In apical view, the shorter rostral side is strongly inflexed at about 120°. The side which forms an interdigitation with the upper latus column is elongated and tapers to a point. The plates of the upper latus column (Fig. 13A) are broadly rectangular, but taper laterally to a downturned process which interdigitates with the plates of the scutal column. The margin which contacts plates of the carinolatus column is squared off, with a short downwardly directed process at the tip. In plates from large individuals, short, laterally directed articular processes protrude from the lower, lateral margins. Plates of the carinolatus column (Fig. 13I, K) are trapezoidal, approximately four times broader than high, and flat. The lateral margins diverge apically. The plates of the carinal column are rectangular, slightly asymmetrical and weakly convex. The apical margin is sigmoidally curved, and the growth lines on the upper part of the plate parallel the margin.

**Remarks.** *Metaloriculina norvicensis* sp. nov. differs significantly from *M. stramentoides* sp. nov. in carinolatus and scutal morphology. In the former there is a discrete tergal surface on the carinolatus, absent in *M. stramentoides* sp. nov. The scutum lacks a pointed apex.

Subfamily *Stramentinae* Withers, 1920 nom. corr.

**Diagnosis.** Stramentinae in which the contact between the carinolatus and tergum is set obliquely at 45–55° to the base of the capitulum; rostral and carinal peduncular plate columns are rectangular and similar in shape, and plates of the carinolatus and upper latus columns interdigitate.

**Remarks.** The discovery of the complete morphology of *Loriculina*, in particular the very distinctive rectangular tergum, which is set subparallel to the base of the capitulum, necessitates separation of the Stramentinae into two groups. The position of the scutal umbo is no longer a useful criterion, because this can be both apical and subapical in forms close to both *Loriculina* and *Stramentum*, so the shape and orientation of the tergum and carinolatus, and the contacts of the peduncular plate columns, are used to define the two subfamilies. Four genera of stramentine are recognized here, namely *Angulatorgum* Hauschke, 1994, *Leweslepas* gen. nov., *Stramentum* Logan, 1897 and *Parastramentum* gen. nov.

**Phylogeny.** During the present study, it became evident that species here referred to *Leweslepas* gen. nov. and *Stramentum* form a stratigraphically constrained morphcline which evolved through the Cenomanian and Turonian (see Fig. 29). The earliest species in this succession is *Leweslepas hauschkei* gen. et sp. nov. from the lower Cenomanian *Mantelliceras dixoni* Zone of Sussex, UK, which has apical scutal umbones and a transverse capitular basal margin (low capitolar angle). This is succeeded by *Stramentum praecursor* sp. nov. from the *Turrilites costatus* Subzone of the middle Cenomanian *Acanthoceras rhotomagensis* Zone, in which the scutal umbones are subapical, but which also retains a transverse capitular base. In the late Cenomanian *Metoicoceras gelslinianum* Zone appears *Stramentum pulchellum*, and this survives into the upper Turonian in the UK, Germany and the Czech Republic. The transitions are accompanied by other minor yet significant morphological changes. *Parastramentum* gen. nov., from the upper Turonian to Campanian, subsequently evolved from *Stramentum*. 
Genus *Angulatergum* Hauschke, 1994

**Type species.** *Scapellum moorei* Hattin, 1977, designated herein.

**Referred species.** *Loricula syriacum* Dames, 1878, and *Loricula texanum* Withers, 1945.

**Diagnosis.** Stramentinae in which the tergum is asymmetrically rhombic, and the growth lines V down towards the basal angle; scutum with high subapical umbo (2–3/10) and short, pointed apical process; upper latus nearly symmetrical isosceles triangle.

**Description.** The overall form in lateral aspect is asymmetrically oval; the capitulum is proportionately tall, and forms about one-third of total body height. The capitular angle is relatively obtuse (75°) and the occludent margin is slightly convex. The rostrum is small, convex and triangular, and occupies one-third of the height of the rostral margin. The rostrum is acute (55°), forms about one-third of total body height. The capitular angle is relatively obtuse (75°) and the occludent margin is slightly depressed. The upper latus is a perfect isosceles triangle, slightly taller than broad, in small individuals, but develops a slight asymmetry in fully grown specimens, with the basitergal angle at 90°. Growth lines on the upper latus are deflected apically adjacent to the tergal margin. The tergum is asymmetrically rhombic in outline, and is divided into two subequal parts along a line running from the umbo to the basal angle, along which the growth lines diverge upwards. The surface of the carinal side of the valve is about half the size of that on the occludent—upper latus surface. The growth lines deflect apically close to the occludent margin, and two weak ridges and an intervening groove run close to, but subparallel with, the occludent margin. The carinolatus has the outline of an obtuse isosceles triangle, of which the longest margin is the tergal, and the valve overlaps the lower part of the tergum. The growth lines deflect sharply upwards close to the tergal margin. The carina is tall and narrow.

The peduncular plates are two to three times as broad as tall, and the carinolatus, upper latus and scutal columns only interdigitate slightly.

**Remarks.** *Angulatergum* is best known from numerous specimens of *A. moorei* (Hattin, 1977) from the middle Cenomanian of Kansas, which form the basis for the description above. Otherwise, the genus is known exclusively from two small individuals, one from the middle Albian of Texas and the other from the Albian of Lebanon, referred to the genus on the form of the tergum.

**Affinities and phylogenetic relationships of *Angulatergum.*** The genus appears to be basal to the Stramentinae because the occludent and carinolateral margins of the tergum are subparallel as in Loriculinae, and the scutal umbo has a high position. *Angulatergum* perhaps shared a common ancestor with *Leweslepas* gen. nov., with which it shares the large overlap of the tergum by the carinolatus, the upward deflection of growth lines on the tergum close to the carinolateral margin and the low capitular angle. This deflection and overlap are not present in *Stramentum.* *Angulatergum* ranges from the middle Albian to the middle Cenomanian, which supports its inferred basal position.

***Angulatergum moorei*** (Hattin, 1977) (Fig. 15)

1977 *Stramentum moorei* Hattin: pl. 3, figs 1–12, pl. 4, figs 1–24.

**Material.** The holotype (KU 111588) and paratypes (KU 111589–111619, KU 111635–111660) are all from a single lens 1.7 m above the base of the Lincoln Member, Greenhorn Limestone, Bunker Hill, Russell County, Kansas (Hattin 1977). Middle Cenomanian, *Plesiaceantheeras wyomingense* Zone.

**Diagnosis.** *Angulatergum* in which peduncular plate columns are only weakly interdigitate, and the upper margin of the median column is almost flat.

**Remarks.** *Angulatergum moorei* differs from both *A. syriacum* and *A. texanum* in the weaker interdigitation of the peduncular plate columns, and the almost flat upper margin of the median latus column.

***Angulatergum syriacum*** (Dames, 1878)

1878 *Loricula syriaca* Dames: 70.
1884 *Loricula syriaca* Dames; von Zittel: 589, fig. 5.
1935 *Stramentum syriacum* (Dames); Withers: 315, pl. 42, fig. 2.
1994 *Stramentum* (*Angulatergum*) *syriacum* (Dames); Hauschke: 14, fig. 6b.


**Diagnosis.** *Angulatergum* in which the apical margin of peduncular plates of the median column is strongly convex.

**Remarks.** The unique type is a small individual, and the surfaces of the capitular plates are poorly preserved (Withers 1935, p. 316), such that it is not possible to be certain about the precise position of the scutal umbo. However, the tergum with “angles of growth situated almost in the middle of the valve” (Withers 1935, p. 316) are characteristic of *Angulatergum.*
Angulatergum texanum (Withers, 1945)
(Fig. 16E)

1945 Loriculina? texanum Withers: 557, fig. 7.
1994 Stramentum (Angulatergum) texanum (Withers); Hauschke: 14.

**Type.** A small specimen from the Walnut Formation (middle Albian) of Nolan Creek, east of Nolanville, Bell Co., Texas, attached to an ammonite, Oxytropidoceras. 2500, University of Texas collections, Austin.

**Diagnosis.** Angulatergum in which the plates of the median latus, carinolatus and scutal peduncular columns interdigitate strongly, but in which the apical margin of the median column is only gently convex.
Figure 16. Barnacles from the Upper Cretaceous. A, B, *Parastramentum peakei* gen. et sp. nov., cast taken from the interior of peduncle of individual overgrown by an oyster; probable locality ‘Chalk of Norwich, upper Campanian’, T. G. Bayfield Coll., NHMUK 42012; note asymmetry and angulation between peduncular plates of carinolatus (cl) and scutal (s) columns. C, D, *Stramentum alekseevi* sp. nov., holotype, Moscow State University collections, no. 270/22; scutum, external and internal views (original of Alekseev 2009, fig. 4/22a, b); locality 10 of Alekseev (2009), upper Turonian, Mangyshlak, Kazakhstan. E, *Angulatergum texanum* (Withers, 1945), original of Withers (1945, p. 557, fig. 7); Walnut Formation (middle Albian), Nolan Creek, east of Nolanville, Bell Co., Texas; attached to an ammonite, *Oxytropidoceras*; University of Texas Collection no. 2500. F, G, *Parastramentum albertaensis* gen. et sp. nov., photograph (courtesy of Mr Rusty Pimm) and interpretative drawing of holotype, attached to flank of ammonite, *Placenticeras*; Aurora Ammolite Mine, Lethbridge, Alberta, Canada; Royal Tyrrell Museum, Drumheller, Alberta, Canada, TMP 2009.056.0004. Abbreviations: upper latus; cl, carinolatus; c, carinal columns. Scale bars: A–E = 2 mm; F, G = 10 mm.
Remarks. The single small individual is incomplete; the upper half of the scutum is missing, but as Withers (1935, p. 558) noted, the tergum has V-shaped growth lines, confirming its placement in Angulatergum (Hauschke 1994).

Genus Leweslepas gen. nov.

Type species. Leweslepas hattini sp. nov.

Other species. Leweslepas hauschkei sp. nov., L. wrightorum sp. nov., Pollicipes acuminatus Darwin, 1851b, and Scalpellum obsoletum Geinitz, 1875.

Derivation of name. In honour of Don Hattin for his detailed work on North American stramentids.

Diagnosis. Stramentinae in which the umbo of the scutum is apical in position, and the upper latus approximates an acute isosceles triangle in outline. The occludent margin is convex; the growth lines on the carinal lateral margin of the tergum deflect sharply towards the apex, and this region is overlapped strongly by the carinolatus; capitolar angle low.

Remarks. Leweslepas gen. nov. is demarcated from Stramentum, to which L. hauschkei sp. nov. is ancestral, by the apical scutal umbones, the apically deflected growth lines on the carinolateral margin of the tergum, and the strong overlap of the carinolatus over the tergum. In Stramentum, the scutal umbones are subapical to central, the tergal growth lines run straight into the carinal lateral margin, and the contact between the tergum and the carinolatus is narrow, chamfered and flat (Fig. 23O). Leweslepas gen. nov. differs from Angulatergum, from which it probably evolved, in the triangular shape of the tergum, the position of the apico basal line of the tergum close to the carinolateral margin, and the apical position of the scutal umbo.

As discussed above, the distinctive robust scuta with apical umbones and an internal platform above the scutal adductor, which have been traditionally referred to Lori culina, are quite different to the delicately constructed scuta of that genus, and are therefore placed in Leweslepas gen. nov., which has robust scuta with apical umbones. These include Pollicipes acuminatus and scuta from the Cenomanian Unterer Pläner of Saxony and the Turonian Pläner Kalk of Strehlen, close to Dresden in Germany, which are the types of Pollicipes conicus Reuss, 1875 (see also Withers 1935, pl. 40, figs 3—5). The material from the lower Cenomanian Mantelliceras dixoni Zone of Lewes, Sussex, UK, includes two new species of the genus, L. hattini sp. nov. and L. hauschkei sp. nov., which are morphologically very distinct.

Age. Early Cenomanian to early Turonian.
oval–rectangular, and alternate with those of the scutal and carinolateral columns.

**Remarks.** The reconstruction (Fig. 17B) shows the overall form of the species for comparison with other stramentids. The capitulum is low, and the umbones of the tergum, carinolatus and carina all converge; the tergum is partly overlapped by the upper latus and carinolatus. The rostrum is larger than in any stramentid other than *Blastolepas*. *Leweslepas hattini* sp. nov. differs from *L. hauschkei* sp. nov. in the larger rostrum, the shape of the scutum, the shorter occludent margin of the tergum and the taller, narrower carinolatus. It differs from other species of the genus in its strongly convex scutum, with a convex occludent margin.

**Leweslepas hauschkei** sp. nov.  
(Figs 17C, D, 18B–D)

**Material.** The material comprises four variably articulated individuals on the flank of an ammonite (*Acompsoceras*). The most complete of these is the holotype (OU M K.64093); the others are paratypes (OU M K.64094–6). Lower Cenomanian, *Mantelliceras dixoni* Zone, Bed 62 (Kennedy & Gale, 2018).)

**Derivation of name.** In honour of Norbert Hauschke for his important work on stratifieds.

**Diagnosis.** *Leweslepas* in which the scutum is tall and erect, the rostrum is low and broad, the tergum has a long occludent margin and the carinolatus is low and broad.

**Description.** The holotype individual has split post mortem into a basal region of the peduncle detached from the almost perfectly articulated upper peduncle and capitulum, which lacks only the carina (Fig. 18C). The occludent margin is convex, and the triangular rostrum is broader than high. The scutum is triangular, tall and erect in appearance and the umbo is apically positioned. The rostral angle is acute (63°), the basilateral angle slightly obtuse (105°); the occludent margin convex. The upper latus is nearly an isosceles triangle in outline, but the basiscutal angle is acute, and the basitergal angle nearly 90°. The umbo of the upper latus is positioned adjacent to that of the scutum. The tergum is equilaterally triangular, and the occludent margin is long and straight; the growth lines are deflected apically adjacent to the occludent margin. The growth lines on the lower portion of the plate, adjacent to the carinolateral margin, are also deflected apically, and this region of the tergum is strongly overlapped by the carinolatus (Fig. 18C). The carinolatus has the outline of an obtuse isosceles triangle, in which the longest side is the tergal margin; it is as broad as high. Peduncular plates of the upper latus column are crescentic, apically convex, nearly symmetrical and approximately four times broader than high; they alternate with and interdigitate strongly with plates of the scutal and carinolateral columns. Plates of the rostral column are rectangular, and change from broad and low (uppermost plate, in contact with the rostrum) to taller than broad (fourth plate down from rostrum). The contact between plates of the scutal and rostral columns asymmetrically alternates, and is nearly flat.

**Remarks.** *Leweslepas hauschkei* sp. nov. is most closely comparable with *L. acuminata* in the shape of the scutum, but differs in the more acute rostral angle, and more...
Figure 18. *Leweslepas* gen. nov. A, *Leweslepas hattini* sp. nov., OUM K.38133, holotype; complete individual, attached to flank of ammonite *Acompsoceras* sp.; Lower Cenomanian, Chalk Marl, *Mantelliceras dixoni* Zone, Bed 48 of Kennedy & Gale (in press), Southerham Grey Pit, Lewes, Sussex, UK. B, C, D, *Leweslepas hauschkei* sp. nov.; group of four individuals (D) attached to flank of *Acompsoceras* sp.; the best-preserved specimen (enlarged in C) is the holotype (OUM K.64093), the other three are paratypes (OUM K.64094/C0); B, interior of the scutum of OUM K.64094; Lower Cenomanian, Chalk Marl, *Mantelliceras dixoni* Zone, Bed 62 of Kennedy & Gale (in press). E, *Leweslepas acuminata* (Darwin, 1851a), original figure after Darwin (1851a, pl. 3, fig. 6: “Mus. Flower, believed to have come from the Lower Chalk of Stoke Ferry, Norfolk”), probably Cenomanian; specimen presumed lost. F, *Leweslepas wrightorum* sp. nov., exterior of scutum; lower Cenomanian (*Schloenbachia varians* Zone), NHMUK In. 62539; Lower Chalk, Chalk Marl, Compton Bay, Isle of Wight, UK.; Scale bars: A, D = 5 mm; B = 1 mm; C, F = 2 mm.
obtuse basilateral angle, and lacks the flattened upper lateral surface of that species. It differs from \textit{L. hattini} sp. nov. in the size and shape of the rostrum and scutum, the shape of the tergum (short occludent margin in \textit{L. hattini} sp. nov., long in \textit{L. hauschkei} sp. nov.), and the broad, low carinolatus, which is short and tall in the former. From \textit{Stramentum praecursor} sp. nov., to which it is ancestral, it differs in the apical position of the scutal umbones, the presence of a marked overlap of the carinolatus over the tergum, and the apically deflected growth lines beneath this overlap.

\textit{Leweslepas acuminata} (Darwin, 1851a)  
\textit{(Fig. 18E)}  
1851a \textit{Pollicipes acuminatus} Darwin; 56, pl. 3, fig. 6a, b.  
1935 \textit{Loriculina acuminata} (Darwin); Withers: 304, pl. 40, fig. 1.  
\textbf{Type.} The scutum, figured by Darwin (1851a), from the Lower Chalk (probably Cenomanian) of Stoke Ferry, Norfolk, in the ‘Mus. Flower’ (Darwin 1851a). Current whereabouts unknown; probably lost.  
\textbf{Diagnosis.} \textit{Leweslepas} with a tall, narrow scutum, the basal margin of which is set at right angles to the lower part of the concave upper lateral margin. Prominent growth lines run parallel with the basal margin, and upturn sharply to run subparallel with the tergal margin. The occludent margin is strongly and evenly convex, and the apex is inclined towards the tergum.  

\textit{Leweslepas obsoleta} (Geinitz, 1875)  
1875 \textit{Scalpellum obsoletum} Geinitz: 288, pl. 44, fig. 16.  
1875 \textit{Pollicipes conicus} Reuss; Geinitz: 204, pl. 37, fig. 29, 29a only.  
1935 \textit{Loriculina laevissima} (von Zittel); Withers: 305, pl. 40, figs 3–5 only.  
\textbf{Type.} The scutum figured by Geinitz (1875) and Withers (1935, pl. 40, fig. 4a, b) from the Turonian Pläner Kalk of Strehlen, Saxony, Germany, is selected as lectotype. Collections of the Senckenberg Naturhistorische Sammlungen, Dresden.  
\textbf{Diagnosis.} \textit{Leweslepas} in which the scutum is twice as tall as broad. The occludent margin is gently convex, and the basal margin is angled at 110° to the straight tergal margin.  
\textbf{Remarks.} Although the outline of the scutum is very similar to that of \textit{Loriculina}, the valves were clearly robust, and possessed a shelf above the scutal adductor as shown by Withers’s (1935, pl. 40, fig. 4b) photograph of the interior of a valve, and the species is therefore provisionally placed in \textit{Leweslepas} gen. nov.  

\textit{Leweslepas wrightorum} sp. nov.  
\textit{(Fig. 18F)}  
\textbf{Type.} The holotype is a scutum from the \textit{Schloenbachia varians} Zone (= lower Cenomanian) Lower Chalk of Compton Bay, Isle of Wight, UK. C. W. and E. V. Wright Collection, NHMUK In. 63529.  
\textbf{Derivation of name.} In honour of the late brothers C. W. and E. V. Wright, extraordinary collectors of Cretaceous fossils and celebrated amateur scientists.  
\textbf{Diagnosis.} \textit{Leweslepas} with a very tall narrow scutum, more than three times taller than broad. The basal margin is angled at 50° to the straight tergal margin.  
\textbf{Description.} The scutum (Fig. 18F) is tall and narrow, and has the form of a scalene triangle, with three unequal sides; the gently convex occludent margin is the longest, the basal margin the shortest. The rostral angle is acute (50°), the basilateral angle obtuse (130°). The surface of the valve adjacent to the upper lateral margin is slightly deflected and flattened for articulation with the upper latus. The basal and upper lateral margins are straight, and a shallow, poorly defined groove runs from the apex to the basal margin, subparallel with the occludent margin. The well-marked growth lines run parallel with the basal margin, but deflect sharply towards the apex close to the upper lateral margin.  
\textbf{Remarks.} The high basilateral angle and acute rostral angle separate \textit{L. wrightorum} sp. nov. from other species of the genus. The scutum was very noticeably inclined towards the tergum, far more so than in \textit{L. acuminata}, \textit{L. hattini} sp. nov. and \textit{L. obsoleta}.  

\textbf{Genus \textit{Stramentum} Logan, 1897}  
\textbf{Type species.} \textit{Pollicipes haworthi} Williston, 1896, by subsequent designation of Withers (1920, p. 68).  
\textbf{Diagnosis.} Stramentinae in which the scutal umbum is subapical to central in position; the tergum is flat and triangular with transverse growth lines parallel with the upper lateral margin which reflexes apically close to the occludent margin; carinolatus and tergum do not overlap, and growth lines on the tergum are not deflected at the carinolateral margin.  
\textbf{Remarks.} Many of the long-held misconceptions and myths which formerly attended the morphological understanding of \textit{Stramentum} (the split carina, lack of a rostrum, number of plate columns; see Withers 1935) were dealt with thoroughly by Hattin (1977) and do not need further discussion here. An important paper by Hauschke (1994) subdivided \textit{Stramentum} into \textit{Stramentum} (\textit{Stramentum}), characterized by straight growth lines on the tergum, and \textit{Stramentum} (\textit{Angulotergum}) with V-shaped
tergal growth lines. Further important differences are noted here, and *Angulotergum* is therefore elevated to full generic rank.

A number of species of *Stramentum* have been described which are based upon specifically indeterminate articulated material, or incorrectly assigned valves. These include:

2. *Stramentum biciplicatum* Jagt & Collins, 1989, from the upper Campanian of Haccourt, Belgium, is based on a large scutum (Fig. 14C, D; NHMUK In. 63637). However, the obtuse basal—occludent angle, the strong taper to an acuminate apex and the shape of the valve indicate that it is referable to the zeugmatolepadid *Zeugmatolepas cretae* (Steenstrup, 1839). Typical *Z. cretae* from the upper Campanian of Norwich are figured for comparison (Fig. 14A, B).

*Stramentum* shows a stratigraphical evolutionary morphology, the early Cenomanian *Leveslepas hauschkei* gen. et sp. nov. evolving into the middle Cenomanian *Stramentum praecursor* sp. nov., and on into the late Cenomanian—Turonian *S. pulchellum* in western Europe. The lineage split in the early Turonian, and *S. pulchellum* gave rise to *S. canadensis* in the early Turonian, which subsequently evolved into the middle Turonian *S. elegans* (both only known from the Western Interior Basin of North America). Similarities in scutal structure allow one to infer that *S. elegans*, or a species close to it, was ancestral to *Parastramentum* gen. nov., which appears in the upper Turonian and continues to the end of the Campanian. *Stramentum pulchellum* continued into the upper Turonian in the UK, while *S. inconstans*, from the lower Turonian of Nigeria, probably evolved from *S. praecursor* sp. nov., and *S. haworthi* from the Santonian of Kansas also probably represents an offshoot of *S. pulchellum*. Detailed evidence for the relationships are discussed with regard to individual species.

*Stramentum* can be divided into a number of precisely defined species using the shapes of the capitular valves, particularly the tergum and scutum, but also the upper latus and carinolatus. Most of the North American species were thoroughly described by Hattin (1977) and these are only reviewed briefly here. *Stramentum haworthi* from the Santonian Niobrara Chalk of Kansas is refuged and redescribed on the basis of extensive material in the NHMUK collections.

**Ontogeny.** There has been some confusion regarding the identification of ‘young’ and ‘fully grown’ specimens of stramentids. For Withers (1935), small individuals were identified as young ones, such as the small specimen of *S. pulchellum* he figured (Withers 1935, pl. 41, fig. 1), and the small type specimens of *Loricula* spp. (see above). However, new peduncular plate rows were evidently generated throughout life, because the largest specimens known show incipiently developed, new plates forming at the junction with the capitulum (Fig. 19C). The number of peduncular plate rows can therefore serve as a useful proxy for the relative age of individuals. This was tested by cross-plotting the number of plate rows in the upper latus column against the total height of articulated individuals, which shows a straight line correlation for *S. pulchellum* and *S. inconstans* (Fig. 21).

Ontogenetic change in *Stramentum* is best known in *S. pulchellum* (see Hauschke 1994), and is also seen in *S. elegans* (Hattin 1977, pl. 1, figs 4–6; refigured here as Fig. 24) and *S. inconstans* (Fig. 22A, C–G). There are a number of ontogenetic changes which are consistent between some species, including increase in number of peduncular plate rows. The upper latus column plates show three distinct ontogenetic stages (Fig. 21C):

- **stage A:** characterized by progressive increase in width and slight gradual increase in height (first 10–12 plates);
- **stage B:** plates retain constant and maximum breadth and height (about 10 plates);
- **stage C:** width and height decrease (last-formed 4–5 plates in the largest individuals known), and the plates become slightly slanted down towards the rostral side (Figs 19C, 21D, 24B, C).

Plates in the s and cl columns also show corresponding A and B stages, but retain maximum width through stage C, during which the plates decrease progressively in height. The stages must relate to discrete phases in life history, and the presence of stage C can be taken as an indicator of fully grown individuals, rather like the crowding of septa towards the body chamber seen in adult ammonites (Kennedy & Cobban 1976). This is very useful because it permits an assessment of age and maturity additional to plate row numbers. Thus, the small specimen taken as holotype of *S. praecursor* sp. nov. can be shown to be fully mature as it has reached stage C, rather than representing a young individual (see Withers 1935).

In addition to these overall similarities, species of *Stramentum* show individually distinctive ontogenetic trajectories which have taxonomic significance, discussed below.

**Stramentum praecursor** sp. nov.

(Figs 19D, 20B, C)

vp. 1935 *Stramentum pulchellum* (G. B. Sowerby); Withers: pl. 41, fig. 1 only.
Type. Holotype is the complete, well-preserved individual figured by Withers (1935) and Hattin (1977), SM B.8935. No locality details. The specimen is attached to an ammonite, Acanthoceras rhomagonese, and came from the Turrilites costatus Subzone, level of couplets C5 to C11 of the Lower Chalk (Gale 1995) in Kent or Sussex, where A. rhomagonese is common and well preserved. The paratype is a smaller specimen also attached to A. rhomagonese, inferred to be from the same level at Glynde, near Lewes, Sussex, UK, BM 00686.

Other referred material. The five individuals attached to Acompsoceras sp. from the Craie de Rouen, Acanthoceras rhomagonese Zone of Cauville, Normandy, France, almost certainly belong to this species, as the scutal umboes are subapical in position (Breton & Boiné 1993), MHNH 8708.

Origin of name. From the Latin praecursor, to go before, as it is the oldest species of the genus.

Diagnosis. A small species of Stramentum in which the peduncle is proportionately low and broad; the capitular angle is low (about 100°) and the rostral angle of the scutum is acute. The occcludent margin of the scutum is strongly convex.

Description. The holotype is complete and well preserved, but there is minor displacement of the uppermost plates of the upper latus peduncular column. Additionally, the surface has been coated with a glue-like substance which obscures some features. Body form is low and squat, and is only slightly taller than broad. The base of the capitulum is set transversely and the capitular angle is high; the occcludent margin is gently convex. The rostrum is small, low and triangular, the scutum rhomboidal. The scutal umbo is positioned subapically (3/10), and the occcludent margin of the scutum is evenly convex, the umbo inconspicuous. The rostral angle is very acute (45°), the basilateral angle is obtuse (125°) and the apex is acutely pointed. The outline of the upper latus is a right isoceles triangle, in which the basitergal angle is about 90°, and the tergal margin is slightly longer than the other two margins. The tergum is triangular, the occcludent margin is slightly convex and the carinal lateral margin is straight, without overlap by the carinolatus. The outline of the low carinolatus is a right triangle, with a carinobasal angle of 90°; the carinal margin is short, and the carina is tall and narrow and tapers gradually to the (broken) apex.

Peduncular plates of the upper latus column are approximately symmetrical, strongly imbricated, have an elongated trapezoidal form, and are three to six times broader than tall. The plates of the carinolatus and scutal columns are three to five times broader than tall and asymmetrical, with a flat or slightly convex contact with the rostral and carinal columns and an elongated, strongly interdigitating contact with the upper latus column. The rostral and carinal columns comprise rectangular plates alternating asymmetrically with the adjacent columns, such that a longer upper face contacts the higher plate of the adjacent column, and a short contact is made with the lower plate.

Remarks. Withers (1935, pl. 41) thought that the holotype specimen was a young individual of Stramentum pulchellum, presumably on account of its small size. However, it possesses at least 18 peduncular plates in the central upper latus column and is therefore fully grown. Additionally, the ontogeny of S. pulchellum is now known (see below), and the specimen bears little resemblance to juveniles of that species (Fig. 21A, B; Hauschke 1994). Stramentum praecursor sp. nov. is intermediate in morphology, and age, between Leweslepas hauschkei gen. et sp. nov. and Stramentum pulchellum. It differs from the former in its possession of a nearly central (rather than apical) scutal umbo, and in the form of the tergum, which is not overlapped by the carinolatus, and lacks the apically deflected growth lines on the tergum found in Leweslepas gen. nov., close to the carinolateral margin. It differs from S. pulchellum in the lower capitular angle, the shape of the upper latus, and the elongated form of the scutum, which has an acute rostral angle and a very obtuse rostrolateral angle. Also, the occcludent margin of the scutum is markedly more convex.


1843 Loricula pulchella G. B. Sowerby Jr: 260, figs 1, 2.
1851a Loricula pulchella G. B. Sowerby: Darwin: 81, pl. 5, figs 1–4.
1858 Loricula MacAdami Thomson: 322, text-fig.
1878 Loricula gigas Fritsch: 147.
1887 Loricula pulchella Sowerby, var. gigas and var. minor Fritsch & Kafka; 1, pl. 1.
1908a Loricula darwini H. Woodward: 493, fig. 1.
1920 Stramentum pulchellum (G. B. Sowerby); Withers: 70, pl. 3, figs 1–3, 264, fig. 1.
1935 Stramentum pulchellum (G. B. Sowerby); Withers: 316, pl. 41, figs 1–4 only, pl. 42, fig. 1.
1937 Stramentum pulchellum (G. B. Sowerby); Hattin; pl. 1, fig. 3.
1989 Stramentum pulchellum (Sowerby); Oekentorp: 134, pl. 1, fig. 1, pl. 2, figs 3, 4, pl. 4, figs 1–4.
1993 Stramentum pulchellum (G. B. Sowerby); Breton & Boiné: 20, figs 1, 3–5, pl. 1, figs 1–7.
1994 Stramentum (Stramentum) pulchellum (Sowerby); Hauschke: 15, pls 1–5.
1996 *Stramentum* (S.) *pulchellum* (Sowerby); Wittler: 94.

2011 non *Stramentum* (S.) *pulchellum* (Sowerby); Ifrim *et al.*: 527, figs 5/1–11.

2011 *Stramentum* (S.) *pulchellum* (Sowerby); Hauschke *et al.*: 202, figs 3–5.

2012 *Stramentum* (S.) *pulchellum* (Sowerby); Schöllmann & Hauschke: 64, fig. 5, pl. 1, figs 1–7.

2013 *Stramentum* (Stramentum) *pulchellum* (G. B. Sowerby jnr); Kočová Veselská *et al.*: 153, pl. 1, figs 1–9.

**Figure 19.** *Stramentum pulchellum* (G. B. Sowerby Jr, 1843), lower Turonian Chalk of Cuxton, near Rochester, Kent, UK. A, B, large individuals attached to ammonite *Lewesiceras* sp.; syntypes of *Loricula darwini* Woodward, 1908 (p. 493, fig. 1; also figured by Withers 1935, pl. 41, figs 2, 3), NHMUK In. 9130. C, holotype (original of *Loricula pulchella* G. B. Sowerby Jr, 1843, figs 1, 2; also figured by Darwin 1851a, pl. 5, fig. 1; Withers 1920, pl. 3, fig. 3; Withers 1935, pl. 41, fig. 4), NHMUK In. 59150; this specimen retains its original convexity. D, *Stramentum praecursor* sp. nov., holotype, SM B.8935; attached to ammonite *Acanthoceras rhotomagense*; although there are no locality details, both the preservation and identity of the ammonite indicate provenance from the *Turrilites costatus* Subzone of southern England, probably Kent. Scale bars = 5 mm.
Diagnosis. *Stramentum* in which the occludent margin is straight to slightly convex, and the angle of the occludent margin to the base of the capitulum acute (30°); the scutal umbo is positioned centrally (4/10) and the umbonal angle of the scutum is very high, such that there is no inflection/inflexion of the lower occludent margin at the umbo; the region of the tergum adjacent to the occludent margin forms a discrete flange on which the growth lines deflect sharply towards the apex; the basal margin of the carinolatus is long. The upper latus is a slightly asymmetrical isosceles triangle in outline.

Ontogeny. The ontogeny of this species is the best understood of any *Stramentum*, because the species is known from both tiny individuals of a length of 3 mm (Hauschke 1994, pl. 4, figs 2–4), up to large, fully grown individuals of a length of over 40 mm (e.g. NHMUK In. 9130). General features of this ontogeny are (Fig. 21):

1. There is little proportional change in shape of the capitular plates during later ontogeny (i.e. once all the capitular plates have formed), or of the capitular angle. The basal margin of the carinolatus becomes proportionately longer, and the length of the contact with the upper latus increases.
2. The peduncular plates increase progressively in number with growth (Fig. 21); they become proportionately lower and broader, and the successive phases of growth pattern (A, B, C; see above) are characterized by a gradual width increase in the A phase (about 12 plates) and a long B phase (10 plates).

Comparison with other species. *Stramentum pulchellum* is closest to *S. praecursor* sp. nov., from which it probably descended, and differs principally in the taller, narrower form of the fully grown peduncle, the higher capitular angle (110–125°), the less acute rostral angle of the scutum, and the proportionately taller upper median and carinolatus. *Stramentum pulchellum* differs from *S. inconstans* in the lower carinolatus, the taller upper median latus, and in the shape of the scutum (less obtuse basilateral angle, more obtuse rostral angle). It differs from *S. canadensis* in the more obtuse umbonal angle of the scutum, the lower upper median and carinolatus, and the lower, broader peduncular plates.

Distribution. This species name has been used widely for diverse stramentid taxa, sometimes without regard to the detailed morphology (e.g. Breton & Boiné 1993; Vega et al. 2007; Ifrim et al. 2011), and it is therefore necessary to assess records of the species in order to obtain an idea of its real geographical and stratigraphical distribution. Accepted occurrences are as follows:

1. South-east England. Three articulated specimens from the lower Turonian *Mammites nodosoides* Zone at Cuxton, near Rochester, Kent, NHMUK In. 59150, In. 9130 (two specimens). A single tergum from the upper Turonian *Holaster planus* Zone of Froxfield, Hampshire (Fig. 23O, P), SM 76163.
2. Northern Ireland. A single specimen from the Turonian of Black Head Bay, County Antrim, Northern Ireland, the type of *Loricula macadami* Thomson, 1858, Ulster Museum, Belfast, no. 1920-1. (Fig. 20A).
3. Czech Republic, Bohemian Cretaceous Basin. Numerous localities, lower to upper Turonian; material figured originally by Fritsch & Kafka (1887), some specimens of which were refigured by Kočová Veselská & Kočí (2012) and Kočová Veselská et al. (2013). Eight specimens, National Museum Prague, NM 03445–9, 04255, 07132.
4. Westphalia, north-west Germany. Upper Cenomanian, *Metoicoceras geslinianum* Zone, to upper Turonian (see Schöllmann & Hauschke 2012, table 1), approximately 60 specimens in various collections.

*Stramentum pulchellum* is therefore restricted to north-west and central Europe (UK, northern Germany, Czech Republic) and ranges in age from the late Cenomanian *Metoicoceras geslinianum* Zone to the late Turonian *Subprionocyclus neptuni* Zone (approximately equivalent to the *Holaster planus* Zone of the UK zonation). Its geographical restriction is perhaps surprising as the species is found attached to cosmopolitan ammonite species of genera such as *Lewesiceras* and *Collignoniceras*.

**Stramentum canadensis** (Whiteaves, 1889)

1889 *Loricula canadensis* Whiteaves: 190, pl. 26, fig. 4, 4a.
1935 *Stramentum canadensis* (Whiteaves); Withers: 319.

1977 *Stramentum canadensis* (Whiteaves); Hattin: 815, pl. 3, figs 13, 14.

**Type.** The holotype is the individual figured by Whiteaves (1889) and Hattin (1977), from the Favel Formation, Turonian, on South Duck River, Manitoba, Canada, collected by J. B. Tyrrell (1887).

**Diagnosis.** Occludent margin moderately inflexed at level of upper latus; umbonal angle of scutum acute (130°), forming separate upper and lower occludent margins; umbonal position 3/10; basilateral angle of scutum 110°; upper latus, tergum and carinolatus proportionately tall; peduncular plates in paired columns more than three times wider than high.

**Remarks.** This species falls close to *Stramentum elegans*, as noted by Hattin (1977, p. 817), who listed a number of differences. Probably the most important of these are in the shape of the scutum, which in *S. canadensis* has an obtuse, rather than right-angled, basilateral angle, and an acute rostral angle. The latter feature does in fact change with ontogeny in *S. elegans*.
Figure 22. *Stramentum. A–G, Stramentum inconstans* Collins, 1986; A, enlargement of capitulum of large individual, NHMUK In. 62059, original of Collins (1986, fig. 2); C, D, large individual, with well-preserved peduncle, NHMUK In. 62161; D, enlargement of peduncular plates on rostral side to show processes on rostral column of plates which alternate with those of the scutal column; E, small individual, NHMUK In. 62055; F, individuals of different sizes and stages of growth, large individual on the left is NHMUK In. 62057; G, holotype (left), NHMUK In. 62053, Lower Turonian, *Mammites nodosoides* Zone of the Eze-Aku Formation of Lokpanta, eastern Nigeria. B, *Stramentum pulchellum* (G. B. Sowerby Jr, 1843), enlarged capitulum of NHMUK In. 19130, the type of *Loricula darwini* Woodward, 1908; Turonian, Cuxton, Kent, UK. Scale bars: A–C, F, G = 5 mm; D, E = 2 mm.
Figure 23. Barnacles from the Upper Cretaceous. A–N, Parastramentum peakei gen. et sp. nov., Belemnella mucronata Zone, New- found Farm Pit, Cringleford, Norwich, Norfolk, UK; A–H, scuta, in external (A, B, E, G, H) and internal (C, D) views to show morpho- logical variation; F shows the distinctive elongated primordial valve; A, holotype, NHMUK IC 1238; B, NHMUK IC 1239; C, NHMUK IC 1240; D, NHMUK IC1241; E, F, NHMUK IC 1242; G, NHMUK IC 1243; H, NHMUK IC 1244; I, J, carinolatera in external (I) and internal (J) views, NHMUK IC 1245, NHMUK IC 1246; K, L, tergum in external (K) and internal (L) views, NHMUK IC1247; M, N, upper latera in external (M) and internal (N) aspects, NHMUK IC 1248, NHMUK IC 1249. O, P, Stramentum pulchellum (G. B. Sowerby Jr, 1843), tergum in external (O) and internal (P) views, Upper Turonian, Holaster planus Zone, Pit no.125 of Brydone (1912), Froxfield, Hampshire, UK, SM 76163; Compare with tergum of Parastramentum peakei gen. et sp. nov. (K, L). Scale bars = 1 mm.
(compare Hattin 1977, pl. 1, figs 4–6). Additionally, the rostral articulation surface is absent in S. canadensis, and the peduncular plates in this species are broader and lower than in S. elegans. The other features noted by Hattin may be partly due to the rather poor preservation of the type specimen of S. canadensis. Hattin interpreted S. canadensis as ancestral to S. elegans, as it is known in Kansas from an older unit (Greenhorn Limestone, Pfeifer Shale Member, lower Turonian) than that in which S. elegans occurs (Fairport Chalk Member, middle Turonian). According to W. J. Kennedy (pers. comm. June 2014), both units fall within the Collignoniceras woollgari Zone of the middle Turonian. In many respects (scutal shape, height/breadth ratio of peduncular plates, apical elongation of carinolatus, upper latus and tergum), S. canadensis is intermediate in morphology between S. pulchellum and S. elegans.

**Stramentum elegans** Hattin, 1977

(Fig. 24)

1977 *Stramentum elegans* Hattin: 807, pl. 1, figs 4–6, pl. 2, figs 1–12, pl. 3, figs 1–12.

**Types.** Holotype is a complete, fully grown individual (Hattin 1977, pl. 1, fig. 4), KU 111520. Fairport Chalk Member, Carlile Shale, Ellis County, Kansas. Middle Turonian, Collignoniceras woollgari Zone. Paratypes from the same locality, KU 111521–111582, KU 111661, FH 8073A–J.

**Diagnosis.** *Stramentum* in which the occludent margin is strongly inflected at the apex of the median latus; carinolatus, tergum and upper latus tall and narrow; scutum trapezoidal, basilateral angle 90–100°, rostral angle 70–80°. Well-developed depressed articulation surface with rostum. Peduncular plates twice wider than tall.

**Remarks.** This species is very distinctive, because of the tall, narrow carinolatus with a short basal margin (e.g. Fig. 24A–D), the tall tergum and upper latus, and the very trapezoidal appearance of the scutum in fully grown individuals (Fig. 24H, J). However, there is considerable ontogenetic variation, and juveniles have lower rostral angles (e.g. Hattin 1977, pl. 1, fig. 5). Hattin (1977) figured beautifully preserved material from the Fairport Member, Carlile Shale of Kansas (middle Turonian, Collignoniceras woollgari Zone), a selection of which are reillustrated here (Fig. 24).

*Stramentum elegans* evolved from the early Turonian *S. canadensis* (see discussion of *S. canadensis* above), and the distinctive morphology of the scutum allows one to infer that this species, or a closely related one, was ancestral to the late Turonian to Campanian *Parastramentum* gen. nov. These features include the nearly right-angled basitergal and rostral angles, the vertical rostral margin, and the well-demarcated rostral articulation surface on the scutum.

*Stramentum elegans* lived benthically, attached to *Inoceramus* and, more rarely, to ammonites (Hattin & Hirt 1991).

**Stramentum cf. elegans** Hattin, 1977

p. 2007 *Stramentum pulchellum* (Woodward); Vega et al.: fig. 5/1–3 only.

p. 2011 *Stramentum pulchellum* (Woodward); Ifrim et al.: fig. 5/9–11 only.

**Remarks.** The small stramentids from the lower Coniacian of Mexico, attached to *Forresteria*, referred to *Stramentum pulchellum* by Vega et al. (2007) and Ifrim et al. (2011), are close to *S. elegans*, on account of the inflected occludent margin and the tall, narrow carinolatus and tergum, and are here referred to *S. cf. elegans*.

**Stramentum haworthi** (Williston, 1896)

(Figs 25, 26)

1896 *Pollicipes haworthi* Williston: 243, pl. 36.

1897 *Stramentum haworthi* (Williston); Logan: 188.

1897 *Stramentum tabulatum* Logan: 189.

1898 *Stramentum tabulatum* Logan: 499.

v 1920 *Stramentum haworthi* (Williston); Withers: 68, pl. 4, figs 1–3.

v 1935 *Stramentum haworthi* (Williston); Withers: 320, pl. 42, figs 3–5.

**Types.** The original specimen of Williston (1896) is an individual (KU 8323) attached to an oyster (Withers 1935) from the Smoky Hill Chalk Member, Niobrara Chalk, near Gove City, Gove County, Kansas, which was refigured by Hattin (1977, pl. 1, fig. 1).

**Material.** The NHMUK collections contain an extensive suite of over 40 specimens of *S. haworthi*, purchased from H. T. Martin in 1900, from the Niobrara Chalk, horizon with *Uintacrinus socialis* (upper Santonian) of Elkader, Kansas. Some of these were figured by Withers (1920, 1935).

**Diagnosis.** Occludent margin weakly inflexed at upper part of scutum, scutal umbo subcentral (6/10); apical quarter of lateral margin of scutum forming discrete, angled facet, and growth lines deflecting apically parallel to this; upper latus forms perfect isosceles triangle; tergum nearly an isosceles triangle, growth lines at occludent margin only deflect slightly apically.

**Remarks.** *Stramentum haworthi* is distinguished particularly by the form of the scutum, with a very low, subcentral umbo and a discrete apical lateral margin (Fig. 25A–D). The symmetrical upper latus and nearly symmetrical, low
Figure 24. *Stramentum elegans* Hattin, 1977, Fairport Chalk Member of the Carlile Shale Formation, middle Turonian, *Collignoniceras woolgari* Zone, Kansas. **A,** juvenile, Hodgeman County, KU 111522. **B,** paratype, original of Hattin (1977, pl. 1, fig 6), Osborne County, KU 8073-A. **C,** holotype, original of Hattin (1977, pl. 1, fig. 4), KU 111520, Ellis County. **D,** group of specimens attached to *Inoceramus* shell; external growth lines run from the top to the bottom. **E,** interior of tergum, original of Hattin (1977, pl. 2, fig. 6), Ellis County, KU 111576. **F,** interior of scutum, original of Hattin (1977, pl. 2, fig. 11), Hodgeman County, KU 111661. **G,** paratype, original of Hattin (1977, pl. 1, fig. 5). **H,** slightly disarticulated individual showing rostrum and paired scuta. **I,** individual showing interior of tergum, original of Hattin (1977, pl. 2, fig. 7), Ellis County, KU111569. **J,** large scutum, unregistered. Scale bars: A, D, H, I = 2 mm; B, C, E–G = 5 mm.
tergum are also characteristic. It most similar to *S. pulchellum*, but differs in details of shape of the capitular valves.

The specimens of *S. haworthi* are all attached to the flanks of poorly preserved composite moulds of large, smooth baculitid ammonites (Fig. 26), as noted by Withers (1935). The most complete of these ammonites (NHMUK In. 18989) is 240 mm in length and 40 mm in width. The cirripedes are concentrated close to the mid-line of the ammonite flanks, and none are present towards the dorsal or ventral margins. Eighteen individuals are present on NHMUK In. 18989, the preferred attachment sites close to the mid-flank of all specimens is suggestive of site selection by settling cyprid larvae. Secondly, it is probable that both sides of the baculitids were colonized, but this is impossible to demonstrate certainly without any counterparts.

Figure 25. *Stramentum haworthi* (Williston, 1896). A, individual showing interior of peduncular plates, only the capitular plates remain of the upper side; NHMUK In. 22640. B, two small individuals in similar preservation, probably in life orientation; NHMUK In. 21940. C, exceptionally well-preserved individual, all plates intact except base of peduncle; NHMUK In. 15945, original of Withers (1920, pl. 4, fig. 3; 1935, pl. 42, fig. 5). D, large individual in common preservational mode, with some disarticulation; NHMUK In. 15945, original of Withers (1920, pl. 4, fig. 2; 1935, pl. 42, fig. 4). All attached to baculitid ammonites, shown in Figure 26. The individual shown in C is at the top of Figure 26C. Niobrara Chalk, horizon with *Uintacrinus socialis* (upper Santonian) of Elkader, Kansas. Scale bar = 5 mm.
Stramentum inconstans Collins, 1986
(Fig. 22A, C–G)


Types. The holotype is the largely complete individual figured by Collins (1986, figs 1, 4), NHMUK In. 62053. There are also eight paratypes, NHMUK In. 62454–62061. All are from the Lower Turonian of the Eze-Aku Formation of Lokpanta, eastern Nigeria, which has yielded a diverse assemblage of ammonites indicative of the Mammites nodosoides Zone.

Diagnosis. Rostral margin of capitulum more strongly convex than carinal margin. Scutum trapezoidal, with acute rostral angle (45°) and oblique basal lateral angle (150°); apex acuminate, and a ridge and shallow furrow run from the umbo to the tip of the apex. Upper latus low and broad. Growth lines on tergum deflected towards apex adjacent to occludent margin. Carinolatus narrow and tall.

Remarks. This species is closest to Stramentum pulchellum in the morphology of the capitular plates, particularly in the shape of the tergum. The low scutum, with an acute rostral angle and obtuse basilateral angle, is very similar...
to that of *S. praecursor* sp. nov. The species differs from *S. pulchellum* in the lower scutum, the broad upper latus and the tall narrow carinolatus. Additionally, the peduncular plates in the apical portion of the rostral column possess a carinally directed process that intercalates with the plates of the scutal column (Fig. 22D). This is absent in *S. pulchellum* and *S. praecursor* (Fig. 19). The species probably evolved from *S. praecursor* sp. nov., with which it shares a low scutum and upper latus. The variation noted by Collins (1986) in the form of the upper latus column of peduncular plates appears to be a taphonomic artefact caused by variable post mortem flexion of the peduncle. In some individuals, this resulted in increased imbrication of the plates (e.g. Fig. 22G), such that they appear to be very broad and low.

*Stramentum cf. inconstans* Collins, 1986  
(Fig. 27E–I, L, M, Q, R)

**Material.** Eight capitular valves, and numerous peduncular plates (>25) from the lower Turonian *Mammites nodosoides* Zone, escarpment 3 km north-east of the village of Asfia, 30 km north of Goulmima, Morocco (Kennedy et al. 2008). The material came from the level between 20 and 23 m (see Kennedy et al. 2008, fig. 2). NHMUK IC 1258–1266.

**Description.** Two incomplete scuta are present in the material (Fig. 27E); these have an acute rostral angle (40°), and a distinctive low triangular depression for articulation of the rostrum. The shape of the rostrum is closely comparable with that of the type of *S. inconstans*, but the Nigerian material lacks any specialized rostral surface. The upper latus (Fig. 27I) is low and triangular, and the basal scutal angle is low (50°). Both shape and angles are closely comparable to those in *S. inconstans*. The tergum has the form of a low isosceles triangle, with a long, straight, bevelled margin for contact with the carinolatus, and a weakly convex occludent margin (Fig. 27F, Q, R). The growth lines deflect apically at the occludent margin. The carinolatus is tall with a short basal margin and an acute apical angle; the carinal margin is gently concave, the tergal margin convex (Fig. 27G). The shape is very similar to that of type material of *S. inconstans* referred here (Fig. 22A, E–G).

**Remarks.** The morphology of the isolated valves permits detailed comparison with the Nigerian material. The only significant difference is the presence of a defined rostral articulation surface on the scutum in the Moroccan material, absent in the Nigerian types. The presence of a form close to *S. inconstans* in southern Morocco is interesting, because it provides further evidence of provinciality in the distribution of stramentids, the African records both representing occurrences on the southern side of the Tethys Ocean.

*Stramentum alekseevi* sp. nov.  
(Fig. 16C, D)

2009 *Loricula laevissima* (Zittel); Alekseev: fig. 4/22a, b.

**Holotype.** The scutum figured by Alekseev (2009), upper Turonian, Locality 10, Mangyshlak Peninsula, Kazakhstan. Moscow State University collections, no. 270/22.

**Diagnosis.** *Stramentum* in which the scutal umbo is positioned high on the occludent margin; the lateral and rostral surfaces are depressed, and the scutal adductor scar is deep and high in position.

**Description.** Scutum triangular, occludent margin long and convex. Rostral angle acute (60°), basilateral angle obtuse (110°). Umbo subapical (2/10) and very high. Rostral surface very broad and tall. A depressed triangular zone adjacent to the upper lateral margin extends from the basilateral angle to the umbo. Distinct growth banding is present on the exterior of the valve. On the interior of the valve, the scutal adductor scar is high and deep, with no supra-adductor shelf.

**Remarks.** This form is referred to *Stramentum* with some uncertainty because the high scutal umbo and the deep, very high position of the scutal adductor are not typical of the genus. However, it shows an overall similarity to *S. elegans*, in the development of depressed lateral and rostral surfaces (compare Fig. 24H, J), and in the shape of the scutum of immature *S. elegans* (Fig. 24A).

**Genus Parastramentum** gen. nov.

**Type species.** *Parastramentum peakei* gen. nov.

**Other included species.** *Loricula expansa* Withers, 1911, *Parastramentum albertaensis* sp. nov. and *Parastramentum brydonei* sp. nov.

**Derivation of name.** From the Sanskrit *para*, meaning beyond, the genus having presumably evolved from *Stramentum*.

**Diagnosis.** Body asymmetrical, inclined towards rostral side; peduncular plates angled to mid line, scutal and carinolatus columns differ in shape and orientation; scutum rhombic, umbo central or slightly subcentral; sharply demarcated, inset, triangular rostral articulation surface; angle between occludent and rostral margins obtuse, 120–130°; tergum triangular, elongated, occludent surface inwardly curved, angled to rest of valve.

**Remarks.** *Parastramentum* gen. nov. is consistently distinguished from *Stramentum* by the morphology of the scuta, terga and peduncular plates. In *Stramentum*, the tergum has a flat interior surface, and the outline is triangular with gently convex margins (Figs 23O, P, 27F, Q, R). In
Figure 27. Barnacles from the Upper Cretaceous. A–D, J, K, N–P, *Parastramentum peakei* gen. et sp. nov., peduncular plates, *Belemnitella mucronata* Zone, Newfound Farm Pit, Cringleford, Norwich, Norfolk, UK (Wood 1988); compare with reconstruction shown in Figure 28; A, D, plates from upper latus column, NHMUK IC 1250, 1253; B, plate from carinolatus column, NHMUK IC 1251; C, plate from scutal column, NHMUK IC 1252; J, K, N, O, plates from either rostral or carinal columns, NHMUK IC 1254–7; P, plate from unknown position, NHMUK IC 1258. E–I, L, M, Q, R, *Stramentum cf. inconstans* Collins, 1986; E, external aspect of broken scutum, NHMUK IC 1259; F, Q, R, terga; F, NHMUK IC 1260; Q, R, NHMUK IC 1266; G, carinolatus, NHMUK IC 1261; I, upper latus, NHMUK IC 1263; H, L, M, peduncular plates, I, from upper latus column, NHMUK IC 1262, 1264, 1265; E, F, H, I, L, M, Lower Turonian, *Mammites nodosooides* Zone, region of Goulemima, Morocco; G, escarpment 3 km north-east of the village of Asfla, 30 km north of Goulmima, Morocco, equivalent horizon to 20 m and 23 m in Kennedy et al. (2008, fig. 2). Scale bars: A–C, E–I, L, M, Q, R = 1 mm; D, K, N–P = 0.5 mm.
**Parastramentum** gen. nov., the valve is strongly inflexed parallel with the occludent margin, and a separate occludent surface is bent towards the opposing tergum (Figs 14G, H, L, P, 23K, L). The contact with the carinolatus is straight. The scuta are characterized by the fact that the lateral and rostral margins are set at about 90° to the basal margin, and the new genus also shows downward inflexion of growth lines close to the upper occludent margin, an approximately central scutal umbo, and a well-defined inset facet for articulation of the rostrum (Figs 14M–O, 23A–H).

The form of the body is known from two articulated specimens, one from the Bearpaw Formation (Campanian) of Alberta, Canada, here described as *P. albertensis* sp. nov. (Fig. 16F, G), and an individual of *P. peakei* sp. nov. lacking the capitulum, from the upper Campanian Chalk of Norwich, UK, preserved on the basal attachment surface of an oyster (Fig. 16A, B; NHMUK 42012). The peduncle is asymmetrically inclined towards the rostral side (Fig. 16A, B, F, G), and the carinolatus and scutal column plates are very different in shape, the carinolatus column being angled to the upper latus column (Fig. 16A, B, F, G; compare with *Stramentum* in Fig. 19).

The distinctive scutal morphology of *Parastramentum* gen. nov. is foreshadowed in that of *Stramentum elegans*, in which the basal and lateral margins are nearly at right angles, and a distinct rostral articular surface (rostral slip of Hattin 1977) for the rostrum is present (Fig. 24C, H, J). However, the tergum of *S. elegans* is typical of *Stramentum* as it is triangular to rhombic and flat. It is likely that *Parastramentum* gen. nov. evolved from *S. elegans* or a species close to it in the middle Turonian. Terga of *Parastramentum* gen. nov. are present in upper Turonian chalks in the UK, alongside those of typical *S. pulchellum*. *Parastramentum* gen. nov. is locally abundant in upper Campanian Chalk in the UK.

**Parastramentum peakei** sp. nov.
(Figs 14E, M, 23A–N, 27A–D, J, K, N–P)


**Types.** The scutum figured herein (Fig. 23A) from the *Belemnitella mucronata* Zone, *Echinocorys subconica* horizon (see Wood 1988) of Newfound Farm Pit, Cringleford, Norwich, UK (ASG sample no. CR1) is the holotype (NHMUK IC 1238). The other plates figured from the same locality are paratypes (NHMUK IC 1234, 1239–1258).

**Material.** Over 300 isolated plates from the upper Campanian *Belemnitella mucronata* Zone of Norwich, Norfolk, UK; Cringleford, Newfound Farm Pit, Keswick and Catton Grove (Wood 1988). The articulated individual figured by Jagt (2013, fig. 17) is from the Campanian of Hannover, Germany, private collection of W. Dombkski, Ahlten.

**Derivation of name.** In honour of the late Norman Peake, expert on the Chalk of Norfolk, and coauthor of ‘The Upper Cretaceous of Norfolk’ (Peake & Hancock 1961), an important paper.

**Diagnosis.** *Parastramentum* in which the scutum possesses a large triangular, inset, rostral articulation surface. The tergum has an elongated apical region, and the basal angle is not rounded.

**Description.** The scuta (Fig. 23A–H) are asymmetrically rhomboidal in outline, and the basilateral angle approximates to 90° in most specimens, but more rarely is up to 110° (Fig. 23G). The primordial valve (Fig. 23F) is very elongated and triangular, and forms a distinct prominence on the occludent surface (e.g. Fig. 23A, B, G). The occludent angle is obtuse, from 140–160°, and the umbo is central in position. A well-demarcated, triangular rostral articulation extends from just beneath the umbo to the basal margin, and is inset beneath the rest of the valve’s surface. A poorly defined ridge extends from the umbo to the basilateral margin, better defined in larger valves (Fig. 23H). The apical angle is acute (50–60°), and a raised area extending from the umbo to the top of the upper lateral margin, well developed in *P. expansum* (Fig. 14N, O) is weakly developed (Fig. 23A) or absent. On the interior of the valve, the scutal adductor scar is slightly subcentral (Fig. 23C, D). The terga (Figs 14E, 23K, L) approximate in outline to a right triangle, with the upper latus and occludent margins subtending an angle of 90–100° and an acute apical angle. A well-defined, inflexed occludent surface is present on which the growth lines swing sharply towards the apex. The upper latus is flat (Fig. 23M, N), and has a slightly asymmetrical triangular outline, with significant overlap of the tergum and scutum. The carinolatus (Fig. 23I, J) has the outline of an isosceles triangle, of which the rostral margin is the longest, and the basal and carinal margins are subequal in length. On the interior, adjacent to the carinal margin, a flange extends from the apex to just above the carinobasal angle, which presumably articulated with the carina.

The peduncular scales (Figs 27A–D, J, K, N–P, 28) include rectangular carinal and rostral rows (Fig. 27J, K, O, N), often with an extension on the carinolatus side (e.g. Fig. 27O). Plates of the scutal column (Fig. 27C) are low and broad, and have a blunt termination against the carinal column, and an interdigitation with the upper latus column (Fig. 28). Plates of the central upper latus column (Fig. 27A, D) are distinctly asymmetrical, and have lateral processes which interdigitate with both the carinolatus and scutal columns (Fig. 28). The carinolatus column (Fig. 27B) tapers very markedly from a tall blunt rostral margin towards the upper latus column. The
reconstruction (Fig. 28) gives an impression of the form of the peduncular construction, aided by the type specimen of *P. albertaensis* sp. nov. (Fig. 16F, G) which clearly demonstrates the asymmetry between scutal and carinolatus columns characteristic of *Parastramentum* gen. nov. (see also Fig 16A, B).

Remarks. *Parastramentum peakei* sp. nov. differs from *P. expansum* in the better developed, inset scutal articulation, and the absence or very weak development of a ridge on the upper occludent margin. From *P. brydonei* sp. nov., it differs in the more acute basal angle, and narrower basal portion of the valve.

*Parastramentum expansum* (Withers, 1911)  
*(Fig. 14N–P)*

v 1911 Loricula expansa Withers: 27, fig. 8a, b.  
1920 Stramentum expansum (Withers); Withers: 70.  
p. 1935 Stramentum expansum (Withers); Withers: 321, pl. 39, fig. 9.  
vp. 1935 Loriculina laevissima (von Zittel); Withers: 305, pl. 40, fig. 13 only.

Types. The scutum from the ‘Actinocamax quadratus’ Zone (probably either upper *Offasterr pilula* or basal *Gonioteuthis quadrata* zones, lower Campanian) of East Harnham, near Salisbury, Wiltshire, UK, is the holotype (NHMUK In.13812). Three other scuta from the same locality are paratypes (NHMUK In. 30524–6).

Other material. The more completely known *P. peakei* sp. nov. allows assignation of a tergum from East Harnham, identified and figured by Withers (1935, p. 305, pl. 40, fig. 13) as belonging to *Loriculina laevissima* to be correctly assigned to this species (see above). Of the other material assigned by Withers to *S. expansum*, the listed scutum from Norwich (NHMUK In. 27275) is here assigned to *P. peakei* sp. nov.

Diagnosis. *Parastramentum* in which the scutum bears a slightly raised, flat-topped and sharply defined triangular ridge running from the umbo to the upper part of the lateral margin. Rostral articulation surface weakly developed. Tergum subtriangular, apex short, with broad to rounded basal angle.

Description. The four available scuta are large and have a trapezoidal outline, and the rostral and lateral margins are subparallel (Fig. 14N, O). The lateral and basal margins are set at right angles, and the umbones are central to slightly subcentral (5–6/10). The umbonal angle is 135–150°, and the apical angle is 50–60°; a slightly raised, flat-topped and sharply defined triangular area runs from adjacent to the umbo to the top of the lateral margin, on which the growth lines are slightly deflected away from the apex. A poorly defined low crest runs from the umbo to the basal angle, on which the growth lines deflect at 90°. The rostral articulation surface is poorly defined. The single large, damaged tergum (Fig. 14P) is markedly concavo–convex, and subtriangular, and the part of the
valve adjacent to the occludent margin is bent towards the opposing tergum. On this area, the growth lines are inflected towards the apex of the valve. The occludent margin is shorter than the lateral margin, and the carinolateral margin is long and straight. The basal part of the lateral margin forms a short separate margin, set at 90° to the occludent margin.

**Discussion.** *Parastramentum expansum* differs from the late Campanian *P. peakei* sp. nov. in a number of features. On the scutum of the latter the ridge running from the basal angle to the umbo is poorly defined or absent, and the flat, raised area adjacent to the upper part of the occludent margin is absent or poorly defined. The rostral articulation is well defined and inset in *P. peakei* sp. nov. The terga differ in that the occludent margin of *P. peakei* is proportionately shorter, and the basal tergal angle is not truncated by a short separate margin.

It is noteworthy that Withers (1935, p. 322) was not certain of the stramentid affinities of *P. expansum*, stating that “The possibility is not excluded that it may represent a varietal form of *Zeugmatolepas cretae*”. Similarities between zeugmatolepadid and stramentid scuta can now be shown to be convergent.
**Parastramentum albertaensis** sp. nov.  
(Fig. 16F, G)


**Derivation of name.** For the province of Alberta, Canada, where the unique specimen was found.

**Diagnosis.** *Parastramentum* in which the basal angle of the scutum is well rounded, and the scutal umbo is subcentral.

**Description.** The single large (35 mm length) and mature individual is articulated, but the capitular plates are somewhat damaged, and the boundaries of the tergum, carinolatus and upper latus can only be inferred. The scutum is well rounded, and the scutal umbo is subcentral.

**Description.** The single large (35 mm length) and mature individual is articulated, but the capitular plates are somewhat damaged, and the boundaries of the tergum, carinolatus and upper latus can only be inferred. The scutum is well rounded, and the scutal umbo is subcentral.

**Remarks.** This species is referred to *Parastramentum* gen. nov. based on the shape of the scutum, which has a right-angled basilateral angle, and most particularly on account of the shapes of the peduncular plates which can be compared in detail with those of *P. peakei* sp. nov. The species differs from congeners in the shape of the scutum, and not obliquely set. There are well-marked A–C ontogenetic stages, with about 10 plates in the A stage, eight in the B stage and seven in the C stage. The C stage plates become progressively lower in height towards the capitulum, and are slanted towards the rostral side.

**Remarks.** This species is referred to *Parastramentum* gen. nov. based on the shape of the scutum, which has a right-angled basilateral angle, and most particularly on account of the shapes of the peduncular plates which can be compared in detail with those of *P. peakei* sp. nov. The species differs from congeners in the shape of the scutum, and not obliquely set. There are well-marked A–C ontogenetic stages, with about 10 plates in the A stage, eight in the B stage and seven in the C stage. The C stage plates become progressively lower in height towards the capitulum, and are slanted towards the rostral side.

**Remarks.** Withers (1935) identified these plates as terga of *Loriculina*, but the discovery of well-preserved individuals of *Loriculina* shows that they cannot belong to that genus. The terga from Froxfield can be confidently assigned to *Parastramentum* gen. nov. from their elongated triangular shape, and the inturned occludent part of the valve. They are comparable with *P. peakei* sp. nov. in the degree of elongation of the valves, and the acute apical angle, but differ importantly in the more rounded, broader basal angle (compare Fig. 14G, H with Fig. 23K, L). The occurrence is of importance in that it demonstrates that *Parastramentum* gen. nov. had evolved by the late Turonian, and co-existed with typical *Stramentum pulchellum*.

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Supplemental material

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